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MEMOIRS:

Haplodiscus Piger; a new Pelagic Organism from the Bahamas.

By

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With Plate I.

I PROPOSE the name Haplodiscus for a small pelagic organism occasionally found in the tow-net near the island of New Providence, Bahamas.

The specimens found by me were collected between the months of July and November, about fifteen specimens in all having been obtained during this period. As I employed a great part of my time during my visit to the Bahamas in using a tow-net, the creature may fairly be called rare.

The general appearance of Haplodiscus, as seen under a simple lens, is shown in fig. 1. The body is ellipsoidal in outline, the antero-posterior diameter being the shortest. In an average specimen the long diameter measured 1·3 mm., the short 1·1 mm. The dorsal surface of the body is slightly convex; the ventral surface is flat when the animal is at rest, but capable of becoming concave as a consequence of muscular contraction. It is by producing a concavity on its ventral surface that the animal slowly and sluggishly moves through the water; this mode of progression, together with a general superficial likeness to a Protozoon, producing a strong resemblance to the Leptodiscus medusoides of R. Hertwig.

The internal anatomy can only be properly made out by means of sections. In the living animal all that can be seen is a series of three opacities, one at each end and one in the middle of the antero-posterior axis. Of these, the anterior indicates the position of the brain (fig. 1, *Br.*); the median that of the alimentary tract and reproductive glands; while the posterior is due to the presence of the ductus ejaculatorius and vesicula seminalis (fig. 1, *V. S.*). The relations of these various organs can be easily seen in the diagrammatic longitudinal section (fig. 10). Besides the position of these main organs, the presence of large numbers of "yellow cells," scattered irregularly through the tissues, can be seen in entire specimens, whether fresh or preserved.

The body wall is formed dorsally of two, ventrally of three layers. In both cases the outer layer is a cuticle (figs. 2, 3, 4, and 10, *Cu.*), which again differs in structure on the two surfaces of the body. Dorsally it is an apparently structureless or very finely granular layer about 5 μ in thickness, which appears in section somewhat ragged at its outer edge, being sharply marked off internally from the subjacent tissues. On the ventral surface the cuticle (fig. 4) is divided into two layers; an outer, similar in all respects to the whole dorsal cuticle, and an inner (*i. cu.*), which appears in section as a very narrow transversely striated band. Whether this striation was due to the existence of fine pores or not could not be determined.

A muscle-layer seems to be present on the ventral surface only, and to lie immediately beneath the cuticle. In a longitudinal section through the ventral body wall a clear space, filled with some feebly-staining homogeneous material, is seen to lie in this position, and in this space is a row of rounded dots, the cross sections of transverse muscle-fibres (fig. 4, *m. tr.*). In the region of the ductus ejaculatorius some of these fibres can be seen passing inwards to form part of the sheath of that organ, and here there can be no doubt of their muscular nature (fig. 5, *m. tr.*). Occasionally, but very rarely, a nucleus or two can be seen in sections lying in the neighbourhood of the transverse fibres, but outside them (cf. fig. 4); but whether such nuclei belong properly to the muscle-fibres, or whether they are the remains of an ectodermal epithelium which has otherwise disappeared, I have been unable to determine.

Beneath the layer of transverse fibres is a longitudinal layer, which appears to be much less important, its fibres being fewer and farther apart. These fibres seem in section to be connected with irregular, nucleated protoplasmic elements (fig. 4, *m. ep.*), the distinction of which has been perhaps exaggerated in the figure.

The only other muscles of the body are those round the ductus ejaculatorius (figs. 5, 7, and 10), where their structure is more easily seen. In this region every fibre appears to consist of a thin, wavy, contractile portion, often branched at the extremities, and connected near its middle with a granular protoplasmic body, containing a distinct nucleus. These fibres resemble those described in Tænia by Roboz more than any others with which I am acquainted.

A protoplasmic tunic, perforated only by the ductus ejaculatorius, forms the innermost layer of the body wall, lying immediately beneath the cuticle dorsally, but separated from that structure on the ventral side by the muscles. This tunic (figs. 2, 3, 4, 10, *P. t.*) consists of an irregular layer of granular protoplasm, in which nuclei are embedded at frequent intervals, but which does not show any trace of division into distinct cells. From the inner wall of this tunic numerous processes are given off (figs. 2, 3, 4, 10, *P. r.*) which anastomose with one another in the cavity of the body, forming a reticulum which is either continuous with, or forms an investment for, the remaining organs of the animal.

Embedded in the protoplasmic tunic, and opening from it through the cuticle to the exterior, are numerous mucous glands (figs. 2, 3, *gl.*). These are irregular spaces in the tunic, filled with a deeply-staining, probably mucous substance. The glands often contain, besides mucus, the remains of nuclei.

The brain is a transversely elongated body, lying embedded in the protoplasmic tunic at its anterior end of the body (figs. 1, 3, 10, *Br.*). It is composed of a mass of fibres, below which is a layer of nerve-cells. From some of these cells processes go downwards to the cuticle, which some, and probably all, perforate. At each side of the brain is a special group of these processes, which stain more deeply than those nearer the middle line, though they seem not to differ from the latter in any other respect. I unfortunately neglected to make macerated preparations of the fresh Haplodiscus while I was in the Bahamas, and I cannot therefore say more about these processes. There can, however, be little doubt that they are in some way sensory.

A nerve having precisely the structure of the brain goes on each side for a short distance round the edge of the creature.

The alimentary tract occupies the centre of the body, communicating with the exterior by a mouth (figs. 2, 10, *M.*), which is simply a small perforation of the ventral cuticle, round which the muscles and other tissues do not seem to have undergone any special modification. The alimentary tract itself consists of a large mass of protoplasm, continuous at the sides of the mouth with the general tunic of the body, and sending processes from every point to join the protoplasmic reticulum. Nuclei seem to be absent, except occasionally at the edges of the mass. Vacuoles are frequently found, containing generally small crustaceans in various stages of disintegration. In one series of sections the alimentary protoplasm protruded from the mouth as represented in fig. 10, and it seems probable that during life it is capable of forming pseudopodia for the capture of prey.

The reproductive glands consist of a single testis, which lies on the dorsal side of the body, vertically over the mouth, and a pair of ovaries, one on each side of the alimentary mass.

The testis (figs. 2 and 10, *Te.*) is a mass of large, deeply-staining cells, lying in a meshwork of processes of the general reticulum, but not separated by any definite investing membrane from surrounding structures. The cells which form the organ vary in character (fig. 8, *a*—*c*). First are found masses of large, finely-granular cells, the nuclei of which are evidently about to divide, presenting the appearance shown in fig. 8, *a*. Amongst these are masses, one of which is drawn in fig. 8, *b*, which resemble sperm-morulæ, being made up of a number of narrow, elongated pieces of protoplasm, each piece containing an elongated, deeply-staining nucleus, the pieces being spirally grouped around what appears to represent the part of the original cell which remains behind after the formation of spermatozoa. The elements of the third kind (fig. 8, *c*) are free spermatozoa, which lie loosely in a line running from the testis itself to a kind of vesicula seminalis at the posterior end of the body. The spermatozoa are elongated and wedge-shaped, seeming not to be provided with vibratile tails. Their nuclei are apparently always elongated and thread-like, though in most preparations there are individual examples in which no nucleus at all can be detected.

The vesicula seminalis is simply a space in the general somatic reticulum, a little larger than usual, which is filled with spermatozoa; its size varies according to the sexual condition of the animal to which it belongs, but it has not seemed worth while to do more than indicate its position in the diagram (fig. 10).

The ductus ejaculatorius appears to open into the somatic cavity at a point just ventral to the seminal vesicle. It is in the form of a tube, so curved that while its lower half is vertical its upper portion and its internal opening look directly forwards. Near its external opening, which is situated posteriorly in the ventral middle line, the lumen of the duct exhibits a considerable dilatation.

The structure of the walls of the ductus I have not elucidated in a satisfactory manner. So far as I have been able to determine, it is lined by a thick continuation of the ventral cuticle, which, however, exhibits many additional striations and other complications, so as to leave some doubt as to its real nature. Outside the cuticle is a layer of large cells, which may be either an epithelium or more probably a kind of prostate, and outside these is a thick sheath of loosely-arranged muscular tissue, the circular and longitudinal fibres of which appear to be irregularly mixed.

I have given in fig. 10 a diagram only of the structure described, because in actual preparations the course of the ductus is complicated by small secondary twists, perhaps produced by the contraction of the creature in dying, which so complicate sections as to render many figures necessary if any attempt were made to reproduce the appearance actually seen.

The ovaries lie, as has already been said, one on each side of the mouth. Each contains a comparatively small number (under twenty) of ova, which lie loosely near to one another, but only connected as it were accidentally by the general somatic reticulum.

Each ovum consists of a mass of protoplasm, which is granular and deeply-staining in younger, spongy and coloured faintly by hæmatoxylin in older specimens (cf. figs. 2 and 9). The nucleus is large and vesicular, having a reticulum which in most cases breaks up during the preparation of sections, so that the nucleus appears partly filled with a mass of granular detritus. The nucleolus is a remarkable rounded structure, of considerable size, which appears to consist of a homogeneous substance, with a more or less excentric vacuole. The ova are surrounded, at any rate for a considerable time, by a delicate follicular epithelium, distinct from the surrounding reticulum (fig. 9).

No duct of any kind is observable in connection with the ovary, and the only way of escape which suggests itself for the ripe ova is the mouth.

In one specimen an ovum was found in the condition shown in fig. 9, with a large and conspicuous nuclear spindle, and at one end something which might conceivably be a polar body. Whether the dividing nucleus was in this case a preparation for the extrusion of a second polar body or for segmentation could, of course, not be determined, but this observation points to the existence of some method of internal fertilisation as at least probable.

The yellow cells are, as has already been said, scattered quite irregularly throughout the body. In the protoplasmic tunic they are numerous, lying generally freely in a space which separates them from the protoplasm of the tunic itself. This relation is well seen in horizontal sections through the body wall, such as that represented in fig. 6. It is, of course, probable that the space surrounding each cell is a post-mortem effect produced by the action of reagents on the protoplasm. In any case the appearance in sections is constant and characteristic.

There is generally a considerable group of yellow cells above the brain (fig. 2).

No distinct cell wall is discernible in the cells themselves, which appear to consist of a mass of protoplasm, sometimes solid and finely granular (fig. 6), more often vacuolated as in fig. 2. A rounded concretion was often observed in some part of the protoplasm, as in the cell marked γ, fig. 4. The nucleus is always situated close to one end of the cell, and is in sections somewhat coarsely granular.

The systematic position of Haplodiscus is not easily determined. I regret that my limited opportunities of examining fresh specimens did not permit me to form an opinion as to the presence or absence of an excretory system. But if such a system be present, it may fairly be assumed, from its absence in sections and from the general character of the animal, that it is built up on the ordinary Platyelminth type. And, neglecting the excretory system, the other characters of Haplodiscus seem exactly such as might be looked for in a free-living Cestode, which, owing to the absence of a nutrient fluid in which to bathe the surface of the body, and from which to absorb food, had either retained or acquired a mouth.

At the same time it seems easily conceivable that a Cestode or Trematode larva might, either normally or as the result of exceptional surrounding conditions, acquire reproductive glands of a simple type, and such a process would introduce into the life-history of the species in which it occurred a form which might easily present the characters of the animal before us.

EXPLANATION OF PLATE I,

Illustrating Mr. Weldon's paper on "Haplodiscus piger."

List of Reference Letters.

Al. Alimentary mass. *Br.* Brain. *Cu.* Cuticle. *D. E.* Ductus ejaculatorius. *F.* Food particle in food vacuole. *fo.* Follicle cells of ovary. *Gl.* Gland-cell. *i. cu.* Inner layer of ventral cuticle. *m. l.* Longitudinal muscles. *m. l. ep.* Epithelial portion of muscle-fibres. *m. t.* Transverse muscles. *M.* Mouth. *Ov.* Ovary. *P. r.* Protoplasmic reticulum. *Sp.* Sensory processes in connection with brain. *Te.* Testis. *V. S.* Vesicula seminalis. *Y.* Yellow cells.

Fig. 1.—View of Haplodiscus piger, under a simple lens. (× about 40 diam.)

Fig. 2.—Transverse section through the middle of the body, showing the relations of the mouth and alimentary system, the ovaries, and the testis.

Fig. 3.—Transverse section through the anterior end of the body, showing the brain.

Fig. 4.—Small portion of longitudinal section of the ventral surface, showing the structure of the body wall.

Fig. 5.—From a longitudinal section which cut tangentially the sheath of the ductus ejaculatorius, showing the transition between the muscles of the sheath of that organ and those of the body wall.

Fig. 6.—Small portion of a horizontal section through the peripheral protoplasmic tunic, showing the absence of cell-outlines, and the relations of the glands and yellow cells.

Fig. 7.—Two muscle-fibres, from the neighbourhood of the ductus ejaculatorius.

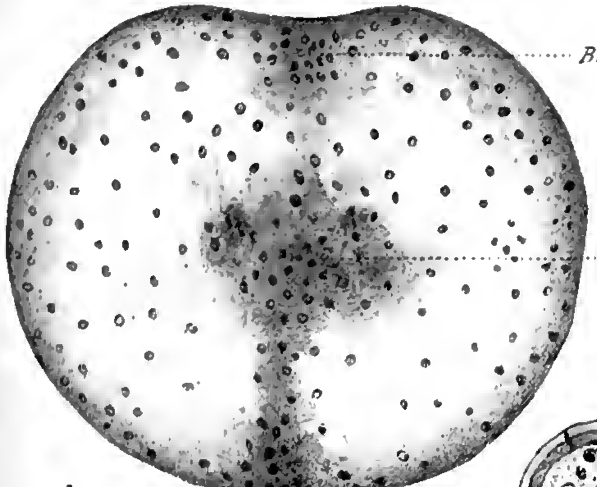
Fig. 8, *a.*—Young sperm-cells from the testis, lying in the general reticulum.

Fig. 8, *b.*—A sperm-morula from the testis.

Fig. 8, *c.*—Ripe spermatozoa.

Fig. 9.—Ovum observed in one specimen, with nuclear spindle and perhaps a polar body.

Fig. 10.—Diagram of median longitudinal section. For the sake of clearness the yellow cells are omitted.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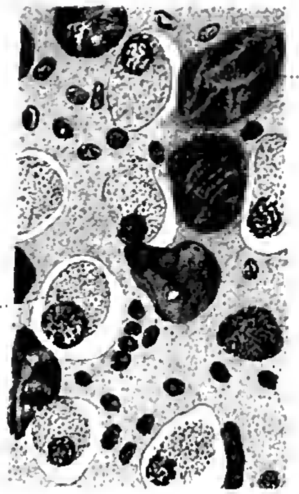
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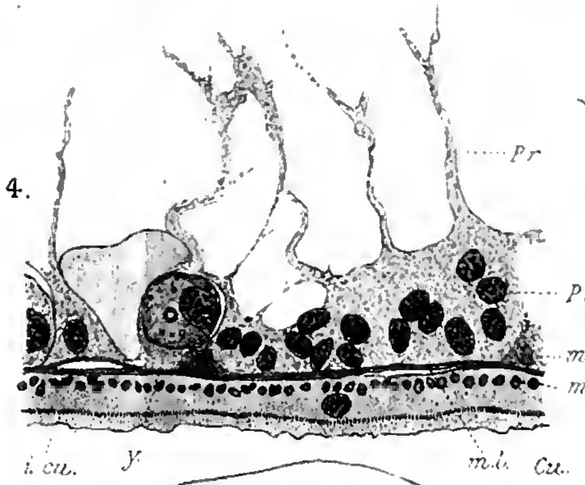
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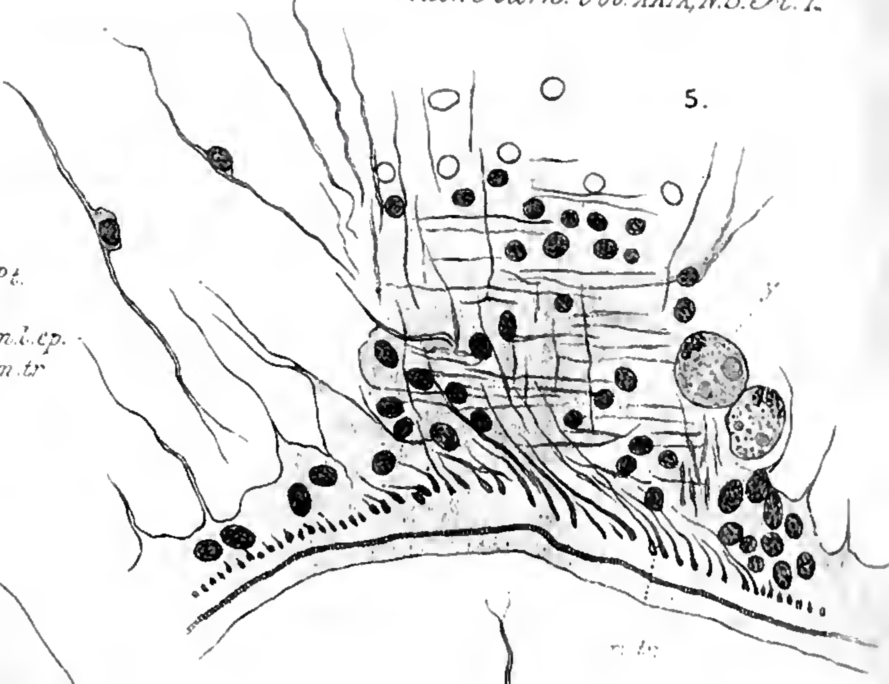
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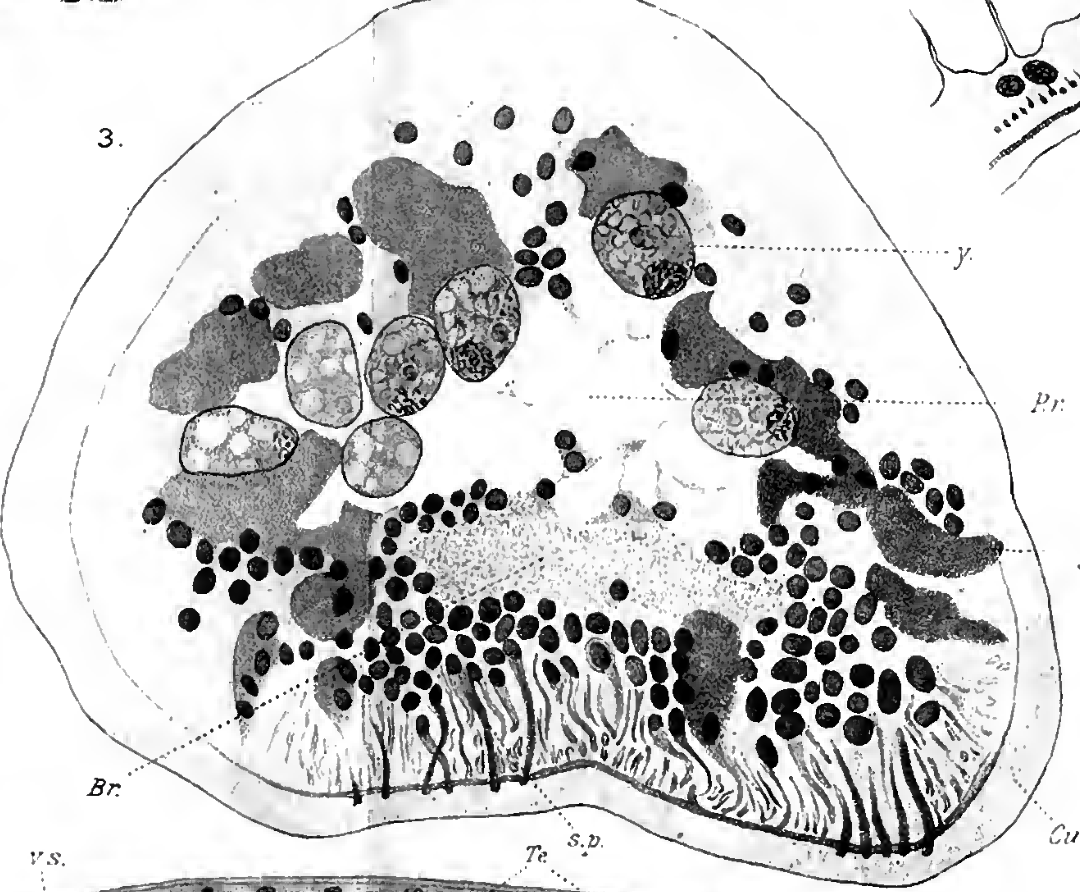
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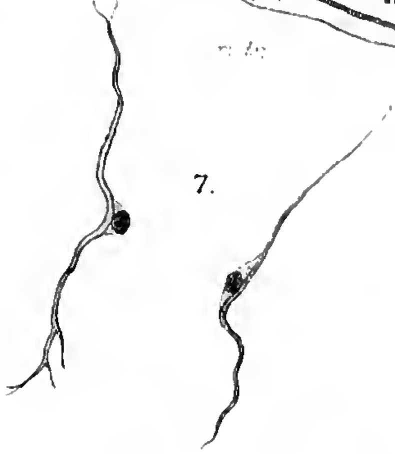
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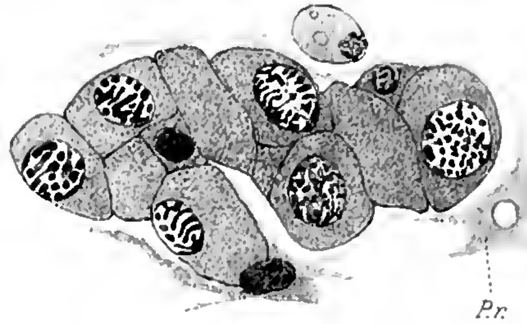
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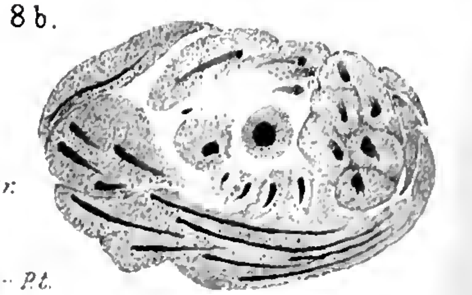
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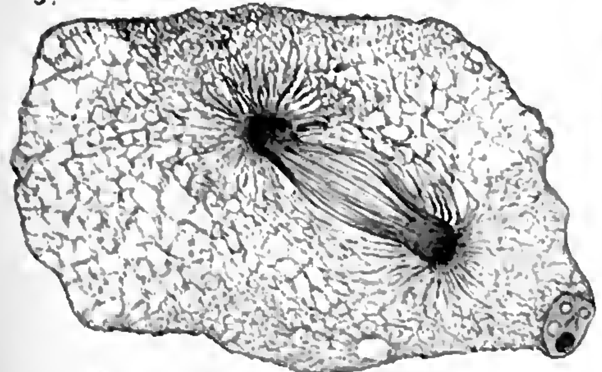
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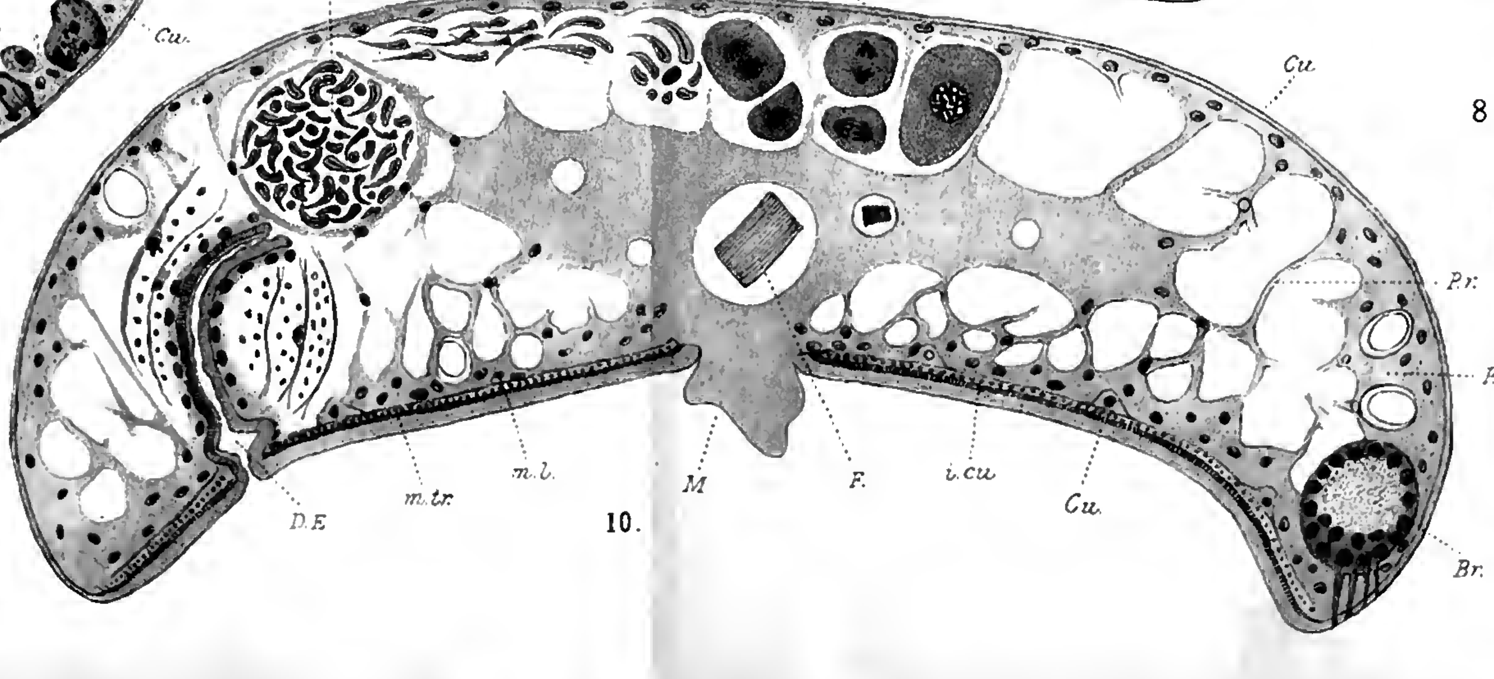
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The True Teeth and the Horny Plates of Ornithorhynchus.

By

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With Plates II, III and IV.

Part I.—The True Teeth.

Historical—Number of the Teeth—Position of the Teeth—Form of the Teeth—Structure of the Teeth: 1. Tooth-papilla or Dentine Germ; 2. Dentine; 3. Enamel; 4. Inner Epithelium of the Enamel Organ; 5. The Stratum Intermedium of Hannover; 6. The Middle Membrane of the Enamel Organ; 7. The Outer Membrane of the Enamel Organ—The Less Developed Fourth Tooth—Conclusions—Future Investigations—Conclusions of Other Writers.

Historical.—The mature Ornithorhynchus has always been described as without true teeth. It is well known to possess eight horny plates, two upon each side of each jaw. The true teeth are developed at an early stage beneath the posterior horny plates, so that some connection between the fate of these latter and that of the true teeth will very probably be found to exist, when material can be obtained.

Although no direct observations have been hitherto made upon the subject of this part of the present paper, several writers have argued that the ancestors of the Monotremes must at one time have possessed teeth. All who follow Hertwig's identification of the mammalian tooth with the placoid scale must believe by implication that this was the case, for the Mammalia must have received their true teeth through those ancestral forms from which the Monotremes, as well as all the higher mammals arose. My friend Professor Howes has called my attention to a paper by Professor Huxley ('Proc. Roy. Soc.,' No. 194, 1879, p. 405), in which the writer, after speaking of the edentulous condition of the Monotremes, expresses the opinion that among the higher Vertebrata there is strong reason to believe that edentulous animals are always modifications of toothed forms. Again, Mr. Oldfield Thomas, in an interesting paper on the teeth of Dasyuridæ and the evolution of mammalian teeth ('Phil. Trans.,' vol. 178 (1887), B. pp. 443—462), quite takes it for granted that the ancestors of Mammalia possessed teeth, and he even attempts to reconstruct the characters of their dentition as far as number, form, and arrangement are concerned. The actual proof of the existence of true mammalian teeth in the specialised descendants of the ancestral mammals is a most satisfactory confirmation of the acute predictions of the writers above-named, and adds another to the numerous proofs of the high degree of probability with which biological speculation may be attended, when based upon the firm ground afforded by the careful consideration and comparison of all available facts.

In the investigation of the epidermic structures of Ornithorhynchus I was greatly aided by Professor Howes, who informed Dr. W. K. Parker of my researches, and induced him to send me a specimen of the young form of this species. Wishing, however, to examine some sections of the bill, which was absent in the specimen forwarded to me, I communicated with Dr. Parker, who most kindly placed the whole of his material at my disposal. With other things, there was a series of transverse vertical sections through the head of another young specimen, which was 8·3 centimetres long in the curled-up attitude in which it had been received, and which was fixed by the spirit. The larger hairs had alone appeared above the skin. Examining these sections on the following day I found that typical mammalian teeth were developing in the upper jaw, the lower jaw being unrepresented in the section. I at once communicated with Dr. Parker, who most generously urged me to publish the fact in the 'Proceedings' of the Royal Society, and greatly assisted me with more material. I received a cleaned skull of the same age, a cleaned left lower maxilla, and the partially cleaned posterior halves of right and left lower maxillæ, and also found in the same bottle a piece of epithelium with the subjacent tissues attached, in which I rightly conjectured that teeth might be embedded. This had probably been removed from the cleaned left lower maxilla. The investigation of this material has afforded the means for this part of the present paper.

A brief account of the structure and mode of occurrence of the teeth was read before the Royal Society, Feb. 9th, and has been printed in the 'Proceedings' (vol. 43, p. 353).

I quote from this paper a passage which insufficiently expresses the extent to which I am indebted to Dr. Parker. "When it is remembered that Dr. Parker had put the sections aside for a time in consequence of the press of other work, intending soon to make use of them for the investigation of the skull, it will be seen at once that my association with this discovery is purely accidental, and that I have been treated in an extremely generous spirit."

Number of the Teeth.—There are certainly three considerably developed and large teeth in each upper maxilla. That this is the case is proved by the comparison of Dr. Parker's consecutive sections, of which the most characteristic are figured in Pl. II, figs. 1—15 × 14·5. It is also most probable that three teeth occur in each lower maxilla, but I can only be absolutely certain of the existence of two, corresponding to the posterior two of the upper jaw. These two lower teeth are figured in Pl. II, fig. 16 × 9, as they appeared in a dissected preparation of the posterior part of the right lower maxilla. Dr. Parker has kindly consented to add this preparation to the odontological series of the British Museum, where it will shortly be placed. The fragment of maxilla came to an end immediately in front of the anterior tooth, so that it was impossible to ascertain whether a tooth corresponding to the anterior upper tooth was present. The part of the opposite maxilla, and the detached fragment of tissue, were cut into consecutive transverse sections; but although some appearances seemed to point to the existence of such a tooth, the condition of the specimens prevented any certainty on the point. Thus the teeth had been greatly injured by the partial cleaning of one specimen, and the other was by no means complete. These conditions did not, however, affect the histological part of the investigation.

Since the account was sent to the Royal Society I have been greatly interested to find an additional tooth, in a very early stage, immediately behind and to the inner side of the posterior tooth, as previously described, in both upper and lower jaws (see Pl. III, fig. 7 × 50). Hence there are traces of four teeth in the upper jaw and probably the same number below.

Position of the Teeth.—These teeth are placed in an antero-posteriorly directed row, exactly as Tomes describes in the development of the typical mammalian tooth, "in a widely open gutter of bone," and the condition of my material indicated that "if at this stage the gum be stripped off from the jaws the developing tooth capsules are torn off with the gum" ('Dental Anatomy,' 1876, p. 134). In the lower jaw no bone had been developed between the teeth and the very large inferior dental nerve which therefore passes along the bottom of the dental furrow; and the same fact holds as regards the superior maxillary division of the fifth nerve and the upper teeth. The posterior upper teeth are similarly unseparated by bone from the closely adjacent muscular tissue lying between the zygoma and the skull. The teeth of both jaws lie in the groove which subsequently holds the posterior horny plates which subserve the function of mastication. At first, when I had only examined Dr. Parker's sections of the skull, I did not think, for reasons which will be given below, that the teeth exactly corresponded to the future site of the plates; but this became certain when I carefully compared the cleaned skull and inferior maxilla with the sections of both upper and lower teeth, and with the dissected preparation. The superficial epithelium shows very little trace of its subsequent differentiation into the plates; it is somewhat thicker than elsewhere, but there are extremely few isolated papillary elevations instead of the very numerous papillæ which are so characteristic in a vertical section of the horny plate. In the upper jaw, the superficial epithelium just external to the anterior teeth is abruptly raised to a somewhat higher level than the rest, suggesting the appearance of the plates; and for a few sections, anterior to the most anterior tooth, this differentiation is continued, the epithelial ridge becoming more pronounced but narrower. In the majority of sections containing teeth there is, however, no marked alteration of level in the epithelium and only a greater thickness. It is possible that the anterior ridge represents the front part of the plates, differentiating especially early; but however this may be, it is quite certain, from the relations to the skull, that the latter correspond to the epithelium covering the posterior as well as the anterior teeth. In many of the twelve anterior sections which contained teeth, there was present beneath this external epithelial ridge, an epithelial tube invaginated from the side, which in transverse section much resembled a very rudimentary enamel germ. The appearance is probably deceptive, for longitudinal and oblique sections showed the existence of a tube, and the transverse sections indicated a distinct, although partially obliterated, lumen between the invaginated and the other walls. It is probably a gland duct, but it is unfortunate that the sections are often incomplete and unsuited for examination in this locality. In the lower maxillæ the epithelium only remained over the teeth, and no raised ridge could be seen, while the relative position of the teeth to the entrance and course of the inferior dental nerve, as compared with the cleaned structure and with the adult jaw, clearly showed that here also the teeth certainly develop in a wide, distinct alveolar furrow, which is subsequently occupied by the posterior horny plate.

Form of the Teeth.—It is only possible to indicate the form of the three anterior teeth, for the fourth is in far too early a stage for any attempt at such description. Successive vertical, transverse sections through the first or anterior upper teeth, beginning anteriorly, are shown in Pl. II A, figs. 1—3. In the lower jaw, I have already stated that I cannot be certain of the presence of this tooth. The sections indicate a long, narrow, very completely calcified tooth, directed downwards and somewhat inwards, the apex being very nearly in contact with the lower surface of the oral epithelium. There is one chief cusp, and apparently a second smaller one, externally placed (shown at Pl. II A, fig. 3, *o. c.*); but I cannot feel very sure about the latter, for the sections of this tooth were not so satisfactory as those of the others. It is quite clear that the tooth is far smaller than the second and third, which lie behind it. These latter are shown for both sides of the upper jaw in figures of a series of vertical transverse sections (Pl. II, B and C, figs. 4—15), and those of the right lower maxilla are seen in a figure (see fig. 16) of a dissected preparation, B being the anterior and C the posterior of the two teeth, seen from within and above. The comparison of B and C in the sections and in fig. 16, at once shows that the anterior or second tooth is a larger tooth than the third· It is also obvious from the figures that each of the second teeth possesses two large calcified cusps (coloured red in the figures), which are placed respectivelyon the anterior and posterior end of the inner side of the upper teeth, and of the outer side of the lower teeth, and which are therefore adapted for interlocking in mastication. The rest of the tooth is uncalcified. The surface (shown in B, fig. 16) is smooth and mammillated, shallow furrows separating the low rounded elevations and ridges. The sections (B, figs. 6—11, *o. c.*) indicate that there are many (probably four or five) small, uncalcified outer cusps in the upper teeth, while the corresponding inner part of the lower tooth (shown in fig. 16) has been accidentally cut away; but there is no doubt that its appearance is, in this respect, very similar to that of the third tooth (fig. 16 C), viz. that its border is crenulated from the presence of small, soft inner cusps, of which only the anterior now remains.

The third tooth, both above and below, differs in the fact that the anterior large cusp is alone calcified, although the posterior cusp is present. Furthermore, the anterior cusp is not so large or so thickly calcified as those of the second teeth. Figure 16, c, shows that five inner cusps are present in the third lower tooth, the central one being very minute. The existence of the same cusps on the outer side of the upper teeth is shown in c, figs. 12—15, *o. c.* Further details of the form of the upper teeth can be learnt from figs. 1—15 on Pl. II, and in the description of the plate. The shape of these teeth is characteristically mammalian, and, together with their position, points to correspondence with some part of the molar series of other Mammalia.

Structure of the Teeth.—The structure is also characteristic of mammalia. The tissues of the three anterior teeth will be considered from within outwards.

1. Tooth-papilla or Dentine Germ.—This is indicated at P in many of the figures in Plates II and III; its structure being entirely normal, and the same may be said of the layer of odontoblasts (*o.*) which form its superficial part wherever dentine is developed. These are well seen in Pl. III, figs. 1 and 2, and in the latter figure the papilla has shrunk, and has therefore drawn the dentinal fibres (*o.f.*) out of their tubes in the dentine. Some of the fibres (*o′.f′.*) remaining fixed in the latter tissue have become stretched to far more than their normal length. I could not determine whether the fibres are processes of the superficial odontoblasts or of deeper cells (as stated by Klein), but the appearance of a conical process with its apex continuous with the fibre, seemed to support the former more common view, for, at any rate, the majority of the fibres.

2. Dentine.—In most cases the tissue appeared homogeneous, but this was a result of decalcification, for sections of tissue which had not been so treated gave the usual appearance (Pl. III, fig. 1, D). I have sometimes noticed the same homogeneity in the decalcified teeth of higher mammals. Although the dentinal tubes did not appear to be very nume-

rous in any of the sections, the number is probably normal, as judged from the retracted fibres seen in fig. 2. The staining of the inner layer of recently formed dentine is peculiar (Pl. III, fig. 1, D′), for as a rule this part of the tissue stains less in reagents. But this is also probably an accidental result, for I noticed that some of the decalcified teeth were normal in this respect. The reticulate outer margin of the recently formed tissue shown in fig. 1 is also peculiar; but here again other sections which had been treated differently showed a margin nearly parallel to the dentine surfaces, such as is usually described. It is noteworthy that the former appearance in the less altered tissue shows a margin which extends irregularly into the calcified dentine, of which parts constricted off and remaining uncalcified would produce the appearances known as "interglobular spaces." The faint oblique lines on the dentine in fig. 1 are probably produced by cracks in the brittle tissue caused by the razor. The decalcified tissue stains deeply (fig. 2); the older part of the more normal tissue remains unstained (fig. 1). Interglobular spaces are represented as black marks.

3. Enamel.—This tissue is of very normal appearance. The prisms are seen in transverse section in Pl. III, fig. 3, and in longitudinal section in fig. 1, E. The line between it and the dentine is very smooth and continuous, while that between it and the enamel cells (fig. 1, *e. c.*) is very irregular. The tisssue stains faintly round the projections of the cells into it, probably on account of less complete calcification. The prisms are oblique to the enamel cells (fig. 1). I could not determine whether each cell exactly corresponds to a prism, but this is doubtless the case. The layer is finely striated parallel to the surface, probably due to the transverse striations of each prism. The prisms must vary in size, for figs. 3 and 1 are magnified to an equal extent.

The layer of enamel is especially thick at the apex of the teeth. It is thinnest on the third tooth.

4. Inner Epithelium of the Enamel Organ—the Enamel Cells.—These are normal, long and thin where

enamel is being formed, much shorter elsewhere (Tomes, l. c., p. 112), They are shown bordering the enamel in Pl. III, fig. 1, *e. c.* Tomes's processes are seen projecting from the inner ends of the cells when torn away from the enamel. The layer is somewhat sharply marked off from the stratum intermedium. In preparing the dissection shown in Pl. II, fig. 16 it was noticed that these cells adhered firmly to the calcified part of the tooth, although they were easily separated elsewhere. The same fact is indicated in many of the figures (1 to 15 on Pl. II).

5. The Stratum Intermedium of Hannover.—Of entirely normal structure and appearance (see Pl. III, fig. 1, *s. i.*). I could not detect capillaries in the layer, as affirmed by Lionel Beale, although they are certainly present in the stellate reticulum, and are sometimes seen very near this layer. Injected specimens would be necessary in order to be quite certain of their absence.

6. The Middle Membrane of the Enamel Organ—the Stellate Reticulum.—This layer is largely developed, and gives to the young teeth a very characteristically mammalian appearance. The extent of the layer, and in fact the relative distribution and thickness of nearly all the layers, is best seen in figs. 1 to 15 (Pl. II). The details of the layer are shown in Pl. III, figs. 1, 4, 5, and 6 (*m. m.* in all figures). It is quite certain that blood-vessels are present in this layer, and that they extend into all parts of it. The presence of blood-vessels in the mammalian enamel organ has been affirmed and denied (Tomes, l. c., p. 127). Klein also states that blood-vessels are not present in the middle membrane ('Atlas of Histology,' p. 185). I have, however, examined some beautiful sections of developing teeth in the rat kindly lent me by Professor Howes, and there is certainly no doubt about the presence of abundant blood-vessels in this layer, in which they had been previously noticed by Professor Howes. In many cases altered blood-corpuscles remained in the lumen of vessels in very large numbers. It is very extraordinary that the existence of such obvious vascular channels should have been denied. I propose

to study the distribution of these vessels in the higher Mammalia by means of injected specimens. In Ornithorhynchus the vessels can be seen entering through the outer layer from the surrounding subepithelial tissues; the same vessel can be traced from the outside into the stellate reticulum (see Pl. III, fig. 4, *c.* and *c'.*). Within the latter the vascular channels are unlike ordinary capillaries, having the appearance of cords of fusiform cells with a very small lumen, which is often difficult to detect (figs. 4 and 5, *c'.*). It seems probable that this abnormality is due to shrinkage, which is in some way connected with the extremely soft and delicate tissue in which the channels are embedded. Thus the change may have followed from the post mortem drying up or absorption of the fluid in the meshes of the stellate reticulum, before the animal was placed in spirit, or, again, it may be connected with the action of the spirit upon vascular walls traversing a tissue which yields them so little support. That the peculiarity is connected with the surrounding tissues seems clear from the normal character of the capillaries in the tooth papilla (Pl. III, fig. 1, *c.*), and in the subepithelial tissues (fig. 4, *c.*); and yet continuity between the channels in the stellate reticulum and the external normal capillaries (fig. 4) clearly indicates the vascular nature of the former. Many appearances seemed to show that channels such as have been represented in the figures—although very numerous—are only the main vessels of the layer, and that a much finer network of smaller vessels is also present. A thin layer of subepithelial (mucosa and submucosa) connective tissue appears to be invaginated with the former system of vessels (Pl. III, fig. 4, *m'.*, which is seen to be continuous with *m.*; also see fig. 5, *m'.*) Such vessels often penetrate in a radiate manner to a great depth, nearly reaching the stratum intermedium. Thus fig. 5 represents such a deep-seated position. It seems probable that the chief vascular invaginations represent a further specialization of the papilliform processes which are well known to invaginate the outer epithelium into the stellate reticulum of the enamel organ (Tomes, l. c., p. 134).

One peculiarity of this layer is the presence of an epithelial nodule situated just beneath the outer layer of the enamel organ, almost immediately over the apex of each calcified cusp of the second and third tooth (see Pl. II, N, in figs. 4, 5, 11, and 12). Nothing of the kind could be made out in the case of the first upper tooth. In thin sections of the lower teeth, prepared for histological examination, the nodule was repeated in many sections, although only shown once or twice in the consecutive sections of the upper teeth represented on Pl. II (for these were prepared for morphological rather than histological work). In some cases there was the appearance of an epithelial cylinder extending from the nodule towards and perhaps reaching the stratum intermedium or enamel cells over the apex of the cusp. It seems clear that the nodule is in some way associated with the chief cusp, for there was always a nodule above each of the latter, while they were never found elsewhere. Further material and probably other stages will be necessary in order to make out the significance of these structures. The minute details are shown in Pl. II, fig. 6, N, where it is seen that the inner cells appear to be corneous and collected into a dense central mass, between which and the outer fusiform cells is a space containing loosely-packed cells resembling the former in character. The position at the extreme edge of the stellate reticulum is also shown.

7. The Outer Membrane of the Enamel Organ or External Epithelium.—This appears to be of normal character; it is a highly irregular and apparently discontinuous layer. Its structure and appearance is sufficiently indicated in Pl. III, figs. 4 and 6, *o. m.* I could not detect the presence of a persistent "neck" continuous from this layer into the oral epithelium but the condition of the less developed tooth, to be described below, indicated that such a neck had existed. It is possible that the process of the superficial epithelium shown in Pl. II, figs. 1, 2, 3, *d. p.*, is a remnant of the "neck." See description of Plate.

The Less Developed Fourth Tooth.—The appearance is shown in Pl. III, fig. 7 × 50, the enamel germ being represented diagrammatically. All the four layers are very distinct; the enamel cells (*e. c.*) are of the normal columnar type, the stratum intermedium (*s. i.*) is very thick, and the stellate reticulum (*m. m.*) is typical although of no great thickness; the cells of the outer epithelium (*o. m.*) have already lost their primitive columnar appearance, and are somewhat flattened. There is a distinct and typical "neck" (not shown in the figure), continuous with the oral epithelium. The tooth-sac and papilla are also normal, and in fact the whole structure is in every way characteristic of an early stage in the development of a mammalian tooth.

Conclusions.—It has been already stated that the teeth of Ornithorhynchus are typically mammalian. The two chief and largest teeth seem to me to resemble closely the multituberculate molar teeth of Myrmecobius. In the lower jaw the resemblance is very striking, nearly all the lower molars of this animal having four small internal cusps and two external cusps, the only difference being in the fact that the internal cusps are the higher, while the outer are higher in Ornithorhynchus. In the upper jaw nearly all the molars of Myrmecobius also have fewer (2—3) cusps on the internal edge, and more numerous (4—6) cusps on the outer edge, and the relative height is also the reverse of that found in Ornithorhynchus.

In addition to the confirmation of the predictions quoted at the beginning of this paper, the typically mammalian character of these teeth confirms in the most striking manner an opinion expressed by Dr. Parker and Mr. Oldfield Thomas as to the ancestry of the Edentata. Thus the latter writes (l. c. p., 458): "In the Edentata on the other hand, we find, as is well known, characteristics wholly at variance with those of all other mammals. In fact a study of the teeth of this order soon induces a belief that the variance is so great as to preclude the possibility of the Edentates lying within the same lines of development as other mammals, a belief that tallies exactly with the conclusions of Professor Parker ('Phil. Trans.,' 1885, p. 116, 'Mammalian Descent,' p. 97, 1885), drawn from the embryology of the group." Mr. Thomas, in Plate xxviii, accompanying his paper, indicates the same argument in a diagram, which shows the Edentate dentition as a side offshoot arising low down from the generalised Prototherian level of the main Proto-meta-eutherian stem.

In the same connection, the present paper bears in an important manner upon Tomes's discovery of an enamel organ in the developing teeth of toothed Edentata (in Armadillo, l. c. 128, 282, 'Quart. Journ. Micro. Sci.,' 1874, and 'Phil. Trans.,' 1876).

Although Tomes did not consider that the presence of the enamel organ proved that enamel had been previously formed in the ancestors of the group, the observation is manifestly consistent with such an interpretation, which is further supported by the conclusions of Oldfield Thomas; and now that an enamel organ and enamel have been proved to exist in a living representative of those ancient mammals from which the Edentates arose, there appears to be little doubt about the significance of Tomes's important discovery. In this statement I am only referring to the existence of an enamel-organ in Edentata, and express no opinion as to the universal presence of this structure independently of the later production of enamel. In order to come to safe conclusions upon this latter fact, it will be necessary to study the development of teeth more widely than has yet been possible throughout the Vertebrate sub-kingdom.

Again, the structure and development of the rudimentary teeth of Ornithorhynchus strongly confirm the opinions of the many writers who hold that teeth are in a more ancestral condition than perhaps any other structure possessed by the adult mammal. While the other higher mammalian organs and structures represented in the Monotremes are profoundly modified in the latter, the teeth remain practically identical in form, structure, and development. We have only to compare the structure of the skeleton or ovary of a Monotreme with that of any other mammal in order to realise how much the identity of the dental structures proves for the excessively ancestral condition of the mammalian organs of mastication. I shall shortly have occasion to show that the very ancient hairy covering of Mammalia is also greatly modified in the Monotremes. As above stated the facts here set forth strongly confirm the identification of the mammalian tooth with the placoid scale.

Again, I have been enabled to suggest a possible explanation as to the meaning of the largely developed middle layer of the enamel organ—the stellate reticulum—which is so characteristic of Mammalia. The condition of these structures in Ornithorhynchus clearly indicates that the association of such a peculiar tissue with teeth of a mammalian form must be very ancient. Tomes (l. c. p. 125, 126) in describing the tissue states, "It has been supposed to have no more important function than to fill up the space subsequently taken up by the growing tooth." I think that a little consideration will show that such a function may be extremely important. It is clear from the method of tooth formation, in which the oldest dentine is the superficial crust, and all additions are upon the inside, that the shape of a mammalian tooth, so far as it is represented by the contour of the dentine, must be modelled beforehand in the soft tissue of the papilla or dentine-germ. This is well seen in Pl. II, fig. 16, c, in which the shape of the tooth is obvious, although only a very small part of the surface is calcified. When the subsequently formed tooth is to be merely conical or of some other simple shape such as is found in Vertebrata other than Mammalia, there is no reason to suppose that the dentine-germ would encounter any difficulty in assuming such a shape, although subject to the resistance of the dense subepithelial tissues. But the case is different when the soft papilla is compelled, as in Mammalia, to assume a complex tuberculate outline; and hence I believe arose the necessity for the existence of a superincumbent tissue of gelatinous consistence, which would exert a pressure only a little greater than that which is necessary to keep the enamel cells in contact with the growing papilla. As a test of the value of this suggestion, it will be of interest to compare the size attained by this layer in the enamel organs of the simple and complex teeth of the same species of animal. At the same time there is as yet no proof that the simple teeth of Mammalia have not possessed a more complex form at some stage in their developmental history.

In Ornithorhynchus the layer is much less developed in the simpler first teeth than in the more complex posterior ones (compare A, figs. 1—3 with B and C, Pl. II). On the other hand, the former are more developed and the layer may have been somewhat reduced in size. It nevertheless contains abundant blood-vessels.

Finally, the existence of such highly developed teeth in the posterior part of the jaws, and the absence of any traces anteriorly, at any rate in specimens of the age examined, seem to clearly indicate that the bill of Ornithorhynchus is a very ancient structure, if not in its present form, at least as some kind of horny beak which could take the place of anterior teeth. I think, however, that it is very probable that the rudiments of teeth may be found anteriorly at a much earlier stage, when the bill is less developed than was the case in Dr. Parker's specimens.

Future Investigations.—In addition to the last-mentioned point, other questions which require investigation are the epithelial nodule in the stellate reticulum, the extent of the capillary network in the latter, the possibility of any further development of the teeth in later stages and their relation to the horny plates, and the presence of an anterior tooth in the lower maxilla. I am now working upon the young stages of Echidna and of the toothless Edentata, and hope to shortly publish an account of the results.

CONCLUSIONS OF OTHER WRITERS.

Since the appearance of the preliminary note in the 'Proc. Roy. Soc.' three writers have published their opinions as to the conclusions which may be drawn from the presence of true teeth in Ornithorhynchus.

Dr. St. George Mivart ('Proc.Roy. Soc.,' vol. xliii, p. 372) is led to reconsider the structural relations obtaining between the Monotremes and all other Mammalia, and between both these groups and the Sauropsida and Amphibia. He concludes that the Monotremes arose from Sauropsidan ancestors, and the higher mammals from Amphibia-like root forms; and that the resemblances which now exist between the higher and lower mammals, including tooth structure, are induced resemblances. In the first place, the existence of true teeth in Monotremes—teeth which Dr. Mivart rightly asserts to be mammalian and non-reptilian in form, and, I may add, in the presence of a strongly-developed stellate reticulum—can hardly be urged in support of this conclusion, for such identity of dental structures strongly favours the converse and more usual theory of a single instead of a dual origin for the Mammalia. In support of his conclusion Dr. Mivart argues for the independent origin of similar structures, and he instances a number of single characters, most of which must be admitted to be truly homoplastic. But many researches of the last few years, leading us to minimise or perhaps to disallow altogether the importance of acquired characters in species construction, tend very strongly against the relative importance of homoplastic as compared with homogenic characters; and the numerous resemblances between the Monotremes and other Mammalia seem to me totally inexplicable on any theory which supposes them to be induced, and the results of a comparatively recent convergence between groups which are fundamentally and in origin distinct.

Especially supporting the usual theory of mammalian origin, is the most important fact that these two groups of mammals bear a constant and definite relation to each other in respect to so many structures represented in both, the relation being such that the structures in question are always primitive, viz. nearer to the lower vertebrates, in the Monotremes, and advanced, viz. further from the lower vertebrates in all other mammals. Any such constant relationship is entirely inexplicable on Dr. Mivart's theory of a dual mammalian origin. Whether the

Monotremes are the descendants of the ancestral Mammalia or not, it is quite certain that the higher mammals must at one time have passed through a condition such as now exists in the Monotremes, in nearly all parts of their organisation; and many powerful arguments can be brought against the assumption that the same stage has been reached independently, and at widely separated periods, in the course of organic evolution. Almost all recent work has strongly supported this argument, the only exception being Gegenbaur's reseaches upon the mammary gland. I have already alluded to my own unpublished work upon the hairs of Ornithorhynchus, which will be found to enforce the argument in a most striking manner. It would, however, be inappropriate to give further supporting details on this occasion. It is sufficient for the purposes of the present paper to again point out that the presence of true mammalian teeth in Ornithorhynchus is, as far as it goes, evidence for the single origin of Mammalia, and against the theory suggested by Dr. Mivart.

Professor H. G. Seeley (' Proc. Roy. Soc.,' vol. xliv, No. 267, p. 129) has suggested that the horny plates of the adult Ornithorhynchus are degenerate true teeth. This statement has rendered necessary the addition of a second part to the present paper, in which the structure of the horny plates is described in detail (see below). There is, however, one part of Professor Seeley's paper which is better considered here. The writer enumerates various characters by which mammalian are usually distinguished from reptilian teeth, and shows that there are many instances in which these characters fail. He applies this argument to the horny plates and to the true teeth of Ornithorhynchus. I shall presently show that the former have structurally nothing whatever to do with true teeth, so that any argument based on such a supposition falls to the ground. I will now shortly prove that the true teeth exhibit all the typically mammalian characters which could be possessed at the stage of development they have reached. Three of Professor Seeley's characters—the presence of distinct sockets, the wear of the crown, and the method of replacement—cannot of course be applied as tests to teeth in such early stages of development. The existence of different kinds of teeth has been proved in the upper jaw, and the presence of many distinct cusps has been abundantly shown. In my short preliminary account alluded to by Professor Seeley (l. c., p. 354, footnote) there is the statement: "The two posterior (upper) teeth have many cusps." In the present paper I think it has been proved that these teeth are not behind those of many mammals which, as Professor Seeley admits, possess "a specialisation which is unparalleled among reptiles." Furthermore, Professor Seeley's suggestion that "there is a certain relation . . . . between the complexity of the crown and the complexity of the fangs" is extremely probable, and leads us to conclude that the developed teeth of Ornithorhynchus must have possessed many fangs. If we finally add the important test of the presence of a highly-developed middle layer in the enamel organ, I think we cannot escape the conclusion that, whatever transitional states may be met with in certain characters of certain teeth in other mammals, these teeth, in the most primitive mammal, show no indications of any such transition, but are essentially and typically mammalian. Of course I entirely agree with Professor Seeley as to the ultimate origin of mammalian teeth from the simpler reptilian type, and I should also agree in considering the differences as comparatively unimportant; and this latter consideration renders it all the more easy to understand how it is that the gap from reptilian to mammalian tooth-structure was crossed before the appearance of Monotreme life at its present level.

Professor E. D. Cope, in 'The American Naturalist' for March, 1888 (p. 259), quotes the description of the form of the teeth from the abstract of my preliminary paper, printed in 'Nature,' February 16th, 1888, p. 383. He considers the subject of great importance in relation to the secondary mammals with multituberculate teeth. He states: "The description reads like that of the dentition of the Plagiaulacid genus Ptilodus. It renders it extremely probable that the

Multituberculata are Monotremata, and not Marsupialia, as has been supposed." Professor H. F. Osborn has also written to me upon the subject, enclosing a proof plate of his 'Memoir upon the Mesozoic Mammalia,' to be published shortly. The second and third teeth of Ornithorhynchus bear considerable resemblance to his figures of the second (lower) molar of Plagiaulax minor and of Ptilodus, except that the two chief cusps of these are on the internal border of the tooth instead of on the external border, as in the lower teeth of Ornithorhynchus. There is also some considerable resemblance to his figures of the teeth of Microlestes and of Bolodon. Certainly, as Professor Cope implies, the character of the teeth of Ornithorhynchus entirely negatives the argument that certain secondary Mammalia must have been specialised relatively to the Monotremata, because of their multituberculate teeth.

PART II.—THE HORNY PLATES OF ORNITHORHYNCHUS PARADOXUS.

Historical—Form and Position of the Horny Plates—Structure of the Horny Plates—Probable Relation of the Posterior Horny Plates to the True Teeth.

Historical.—Home ('Phil. Trans.,' 1802, p. 71) correctly describes these horny plates as differing "from common teeth very materially, having neither enamel nor bone, but being composed of a horny substance only embedded in the gum, to which they are connected by an irregular surface in place of fangs." He describes the "internal structure" as "fibrous, like nail; the direction of the fibres is from the crown downwards." In this description he evidently alludes to the papillæ and columns of softer cells above them, erroneously considering that they represent the hard part of the plate. He also says, "In the smaller specimens before examined each of these large teeth appeared to be made up of two smaller ones, distinct from each other." In this important observation he is alluding to the posterior plates. He wrongly concluded that, in order to attain the adult form of plate, the animal must shed these structures. He found that each cheek-pouch in the female Platypus contained a "concreted substance the size of a very small nut," shown by the microscope to be made up of "broken crystals." The substance was evidently sand; and I have found an even larger quantity in the pouches of a specimen kindly lent me by Professor Moseley. These observations bear in an important manner upon the wear to which the teeth must be subject.

Heusinger ('Histologie,' 1822) wrongly describes Home's "fibres" as "hollow tubes," evidently relying on ground sections of the dried plates, in which the papillæ below and the soft cells above have dried up. This has been a most prolific source of error in the description of these structures, just as it was originally in the case of bone.

Cuvier described the form and position of the horny plates.

Sir Richard Owen ('Odontography,' 1840—1845, vol. i, pp. 309—311) gives an historical account, to which I am indebted for reference to the authorities quoted above. He figures the position of the plates, and somewhat roughly indicates their shape. He describes the form of the teeth, but omits reference to the small third concave surface of the posterior plates in each jaw. He confirms Home's important statement that each of the posterior plates is made up of two separate tubercles in the young animal. "The subsequent conversion of this apparently double into a bituberculate single grinder is produced by the progressive extension and confluence of the bases of the tubercles, not by a process of shedding and the formation of a new tooth, as Home conjectured." He wrongly supports Heusinger's description of hollow tubes, and figures a horizontal (evidently dried and ground) section (vol. ii, pl. lxxvi, fig. 3), which is described as "showing the concentric walls of the canals of the principal tubes, and the minute pores or cells of the denser cementing fibrous substance." The "concentric walls" are the epithelial cells concentrically arranged round the column of soft cells above a papilla; the latter cells, dried up, constitute the "canals of the principal tubes," while the "minute pores or cells" are the dried-up softer centres of the corneous epithelial cells which make up most of the horny plates.

Professor H. G. Seeley, as I have already mentioned, considers that the horny plates are degenerate true teeth. He considers that each of the posterior plates consists of "three teeth on each side closely united together into one long ovate mass." Sir Richard Owen quotes a French analysis showing that the plates consist almost entirely of horny substance. Professor Seeley considers that this "can hardly apply to the posterior teeth," but he gives no evidence in support of such an opinion. He observes that the central concavities of each of the posterior plates is opaque, while the peripheral border is translucent and horny. This appearance is merely due to the fact that the former contains abundant papillæ and columns of soft cells, which dry up and contain air, while these structures are only faintly represented in the latter locality. But the author suggests that the border represents "the uncalcified enamel of the tooth, while the central portion corresponds to the dentine." He gives no evidence, histological or developmental, for the actual occurrence of a structural change so unique as the conversion of uncalcified enamel into dense, translucent horn. Furthermore, I have already shown that the enamel of the true teeth is calcified and hard, and that it has reached a condition which a widespread experience of vertebrate dental tissues proves to be the climax of histological differentiation. Professor Seeley supports his identification of the central parts of the plates with dentine, by describing certain appearances seen in sections which he interprets as due to the presence of bony tissue. If the interpretation were correct it would hardly support the writer's conclusions, for I have shown that the dentine of the true teeth is as typical as their enamel, and has reached a stage of differentiation at which its conversion into bone would be as improbable as the change of enamel into horn.

But Professor Seeley's statement that bony tissue is present in the central parts of the horny plates is only an extreme form of the error which has followed from the exclusive examination of dried and ground-down sections. In Pl. IV, fig. 9, I have shown the appearance of a horizontal section prepared in this way, and it will be seen that there is some superficial resemblance to bone. Sir Richard Owen's "canals of the principal tubes" are Professor Seeley's "large Haversian canals," while the "minute pores or cells" correspond to the "canaliculi" described by Professor Seeley, which radiate from apparent lacunæ. If the more highly magnified fig. 8 be compared with fig. 9, it will be at once seen that the deceptive resemblance to bone is entirely due to the presence of air in the spaces left by the dried-up softer parts, and it will be clear that the whole tissue is typically epithelial. Different sections will include more or less air according to slight differences in preparation, and hence the supposed bone could only be detected "in some specimens." But Professor Seeley can only have looked at horizontal sections of the plates, for the first glance at a vertical section, however prepared (see figs. 4 and 5), would prove that the resemblance to bone was merely delusive. Since the above was written I have been enabled, through the kindness of Professor Stuart, to examine the sections in the Museum of the Royal College of Surgeons, upon which Professor Seeley bases his opinion. They entirely confirm the interpretation at which I had previously arrived, and of which an account is given above. There are several dried and ground-down sections, containing different amounts of air, and those which contain most air are fairly represented by fig. 9. Among them are vertical and oblique sections and horizontal sections with the air displaced. It is difficult to understand how Professor Seeley can have reconciled the appearance of these latter with his interpretation of those horizontal sections which still retain a considerable quantity of air.

Professor Seeley's suggestion that the true teeth may, perhaps, be looked upon as successional to the horny plates may be at once dismissed, for the former not only appear long before the latter can be identified with any certainty, but have reached a very high degree of morphological and histological complexity, as I have shown in this paper and also in the preliminary account in the 'Proc. Roy. Soc.' If, as Professor Seeley supposes, the horny plates are degenerate true teeth, every consideration points to the conclusion that the latter must be identified with the structures which I have described.

Lastly, Professor Seeley considers that the anterior horny plates are still more degenerate and horny "dental ridges," which have become "dental layers formed of vertical parallel plates of horn in which there is no division into separate teeth." I shall presently show that the minute structure of the anterior plates cannot be described in these terms, and that they are neither more nor less horny than the posterior plates, but in every way identical with the latter in structure. Since Professor Seeley's conclusions as to the structure and significance of the horny plates cannot be accepted, it is unnecessary to allude to any of the arguments founded upon such conclusions.

Five years ago I prepared sections of the posterior horny plates, making use of some material kindly given me by Professor Moseley. On making cut and stained as well as ground-down sections, I saw at once that the structures were entirely epithelial, and that previous descriptions of the minute structure had been erroneous. I left the subject until last winter, when I again examined and figured some of the sections, intending to publish them with an account of the other epidermic structures of Ornithorhynchus. At Professor Lankester's suggestion, however, I have added the description and figures of these structures to the present paper, because of Professor Seeley's suggestions concerning them, and also because the posterior plates are evidently connected in some way with the fate of the true teeth, although structurally distinct from the latter. I have also prepared many more sections and have investigated the structure of the anterior plates. I am indebted to Dr. Hickson—Professor Moseley's deputy, and to Mr. C. Robertson for kind assistance in the loan of specimens. The most valuable material, however, was kindly provided by Professor Moseley, the horny plates having been treated with chromic acid in Australia, in 1874. All the other specimens made use of had been preserved in spirit or dried.

Form and Position of the Horny Plates.—The form and relative position of the plates of the upper jaw are seen in Pl. IV, fig. 1, and further details of the upper and lower posterior plates are given in figs. 2 B, and 3 B. Transverse vertical sections of the upper anterior and posterior plates are represented in figs. 4 and 5 respectively. These figures being fully explained in the description of plates it is unnecessary to enter into further details here, especially as the most important points must be again alluded to in considering the probable relation between the true teeth and the plates. The lower anterior plates have not been figured, for they are very similar to those of the upper jaw, the longitudinal ridge being also placed towards the outer margin and the furrow lying between it and the inner margin.

Structure of the Horny Plates.—All the plates possess the same histological structure. They are simply thickenings of the oral epithelium, penetrated in many places by long slender papillæ, each of which sends up from its summit a column of soft, deeply-staining cells, into the stratum corneum. The thickening which forms the plates take place in the stratum corneum, the stratum Malpighii being of normal thickness. The plates are of course continuous on all sides with the oral epithelium. These facts are at once apparent in cut and stained sections, but when the dry teeth are ground down, as in the usual method of preparation, the papillæ and columns of cells dry up and cease to be distinguishable, for each papilla and column forms a single vertical tube full of air, which may be more or less displaced by the mounting fluid, so that the appearances differ greatly in different sections and in different parts of the same section. Such dried and ground-down sections are represented in fig. 5 (vertical) and in fig. 9 (horizontal). The deceptive resemblance of the horizontal sections to bone, is chiefly due to the presence of air in the dried-up, softer, irregularly-shaped centres of the corneous cells which surround the columns. Such minute ramified air spaces bear considerable likeness to lacunæ with branching canaliculi, and their arrangement relatively to the larger air spaces in the dried-up columns of soft cells is also somewhat suggestive of bone (see fig. 9, in which, however, the air of the large central spaces has been almost entirely displaced by the balsam). A vertical section, similarly prepared, at once disposes of the resemblance to bone (compare fig. 5). The true structure is, however, only seen in the cut and stained sections (see figs. 4, 6, 7, 8, 10, 11, and 12, together with their description). The columns of soft cells above the papillæ rise to the surface of the plates, and doubtless assist in promoting the wear of certain parts. Thus the papillæ and columns are very minute or absent in the central ridge of the anterior plates (figs. 4 and 6), and in the raised border of the posterior plates (fig. 5). Conversely, the papillæ, &c., are large and numerous in the concavities of all the plates, and they are seen in fig. 6 to be especially large in the furrow of the anterior plate. The result of their presence is to render the corneous tissue friable, so that its surface becomes irregular as compared with that of the other parts. On examining the vertical sections it was found that the true surface was generally preserved where the papillæ were small or absent, but that it was rarely intact over more than a very short length where these structures were large and numerous. Similar columns of soft cells, also rising from the apex of long narrow papillæ, occur in other dense horny structures of Ornithorhynchus. Thus I have described them in the horny teeth of the tongue ('Quart. Journ. Micro. Sci.,' vol. xxiii, N. S., Pl. XXXII, fig. 7, *l. s.*). The deep surface of the posterior plates is in close proximity to the bone of their alveoli, being separated by a relatively thin layer of connective tissue representing mucosa, submucosa, and periosteum (see fig. 11). The character of the epithelial cells of various parts of the plates may be seen in figs. 8, 11, and 12 (see also description). In some sections of plates which had been softened in an alcoholic solution of caustic potash, after the bone had been softened in dilute nitric acid, the papillæ had been accidentally drawn out of their tubes in the epithelium (by the partial separation of the plates), so that their shape was peculiarly distinct. In many parts of the sections these papillæ formed a fringe along the surface of the subepithelial tissues.

Probable Relation of the Posterior Horny Plates to the True Teeth.—The anterior plates are omitted from this consideration because there is as yet no evidence of the occurrence of teeth beneath them. No epithelial thickening or any other indication of their presence could be made out in Dr. Parker's sections. Certain facts, however, seeem to prove that there is some relation between the posterior plates and the true teeth. These facts are, (1) the lodgment of the plates in the alveolar cavity in which the true teeth appear at an earlier stage; (2) the existence of a certain correspondence between the divisions of the plates, the compartments of the alveoli, and the number of the teeth; (3) the evidence that the plates are developed as at least two separate tubercles, apparently corresponding to the two chief true teeth situated beneath them; (4) the rough correspondence between the shape of the plates and teeth, the chief and higher cusps being internal above and external below, while the chief and higher lateral borders of the upper and lower plates have the same position respectively. On the other hand, the following facts point in an opposite direction:—(1) The possible rudiments of the upper plates in Dr. Parker's sections as epithelial thickenings which do not correspond with the position of the true teeth, but are anterior and external to the latter; (2) the occurrence of the small third concavity at opposite ends of the upper and lower plates, when considered in relation to the true teeth of both jaws.

The first objection may be met by the undoubted fact that the position of the upper plates in the adult corresponds to the position of the true teeth in the young, and not to that of the epithelial thickening. The position of the thickening has already been briefly referred to; it could be distinctly traced on the twelve anterior sections containing teeth, and it gradually disappeared in a few sections posterior to the twelfth. Anteriorly to the teeth it became narrower, but more defined, becoming most distinct in the sixth, seventh, and eighth sections in front of the first section, which exhibited traces of a tooth (see Pl. II, fig. 1). In front of the eighth section it rapidly disappeared. The epithelium of the right ridge in the above-mentioned seventh section is shown in vertical transverse section in Pl. IV, fig. 13, and the appearance strongly suggests an early form of the plate. Traces of papillæ are visible beneath the ridge, and the greater thickness of the epithelium is very noticeable.

I believe that the following account will be found to explain the relation between the teeth and plates, and to reconcile the apparently conflicting observations. The calcified true teeth of Ornithorhynchus became unsuited to the needs of the animal when it adopted a mode of life in which large quantities of sand were necessarily taken into the mouth with the food, when in fact it first fed upon insect larvæ, &c., which it dug with its bill out of the mud and sand at the bottom of streams. The fact that large quantities of sand are introduced with the food has been already proved, and I have noticed that the concavities of the posterior plates are sometimes filled with mud, sand, and the débris of food. At the same time the presence of sand may be valuable in assisting to grind down the food, and it is possible that a store is kept in the cheek-pouches for this purpose, and is intentionally added during mastication. Under such circumstances two things might happen: the true teeth might be protected from the effects of wear by continuous growth from persistent pulps or by a continued succession; or a constantly growing horny plate might be developed from the oral epithelium, and might be substituted for the true teeth. While a corresponding difficulty has been met by the first method almost universally among Mammalia, we must remember that there is no a priori reason why this should be the case. Natural selection only demands relative success and feasibility, and the means by which such success is attained is entirely determined by the character of the variations which appeared at the critical time; so that there is no difficulty whatever in believing that the case has been met by continuous growth in many instances, and by the substitution of another continuously growing tissue in other instances. Ornithorhynchus is not the only example of this method among Mammalia. A similar difficulty, doubtless also caused by the presence of sand and mud in the food, has been met in the same manner in the case of the lower incisors of the Sirenia, which are completely functionless and covered by a horny plate. In the Manatee these true teeth are absorbed early, as in Ornithorhynchus, but in the Dugong they persist until old age, thus proving the entirely independent origin of the horny plate.

We must assume that the chief dental area has been made use of continuously throughout the whole period of change, for the plates are found to occupy the exact position of the teeth. In this manner the muscular and other arrangements upon which the movements of mastication depend would also remain unchanged. We may suppose that the rapidly-wearing true teeth were at first reinforced by an adjacent corneous epithelial thickening in the position of that described in Dr. Parker's sections (Plate IV, fig. 13), and that the thickening gradually extended over the young true teeth, so that these, instead of piercing the epithelium, merely conferred the shape of their crowns upon the latter. Each true tooth was in fact protected by an additional indurated layer external to the enamel. At first the teeth may have been thus protected during the earlier part of the animal's life, coming eventually to the surface. This would take place at successively later periods until they ceased to appear altogether. In strong support of this interpretation is the fact, already quoted, that the two chief concavities of the plates arise separately and fuse at a later period. Each of these separate tubercles would, according to this theory, correspond to one of the two chief teeth in each jaw. A section across the specimen described by Sir Richard Owen would probably settle the question. The anterior small concavity of the upper plate may be similarly formed over the small anterior tooth, or it may represent the epithelial ridge in front of the true teeth. But it must be remembered that the latter is external in position while the concavity is internal. Furthermore, the concavity has its special alveolar compartment, which seems to indicate the former existence of a true tooth. On the other hand, the posterior small concavity of the lower plate is a difficulty on this latter interpretation, for it possesses its compartment, and yet it arises in a position where no small true tooth developes; for it is unlikely that the very rudimentary tooth-germ attains any degree of specialisation; furthermore, there is a corresponding germ in the upper jaw, and yet no concavity. It seems on the whole probable that the alveolar compartments of the small concavities of both upper and lower plates are simply parts of the alveoli for the second and third true teeth respectively, and that the simple anterior tooth does not impress itself on the plate, or, if so, does not produce any effect which can be distinguished from that of the large tooth behind it. Again, the small concavities may be due to subsequent differentiation of the plates. It is quite clear that we cannot be sure as to the correct interpretation of details, although they will be settled with certainty when more material is obtainable. Thus it is certainly possible that the epithelial ridge shown in Pl. IV, fig. 13 may have nothing to do with the plates, and that the latter originally arose over the true teeth only, in the manner described above. But, under any circumstances, the subsequent history appears to be tolerably clear. The true teeth, after ceasing to come to the surface, would be absorbed at successively earlier stages, thus permitting the horny plates to gradually intrude into their alveoli, so that in the adult animal the bone and the under surface of the epithelium are everywhere in close proximity. Many sections in various directions through both upper and lower plates in their sockets failed to reveal any traces of the true teeth, so that absorption is probably complete. The contour of the surface of the plates, originally determined by the underlying teeth, would still be maintained as far as general proportion and arrangement is concerned, because the shape was most favorable for the movements of mastication, which on this theory are supposed to have persisted with little change.

This theory seems to account for all the important facts. Few things would give me greater pleasure than to have the opportunity of testing it, and of being able to produce an exact account of what actually takes place.

DESCRIPTION OF PLATES II, III & IV,

Illustrating Mr. Poulton's paper on "The True Teeth and Horny Plates of Ornithorhynchus paradoxus."

PLATE II.

The upper teeth of both sides are figured in the series of vertical transverse sections forming Figs. 2—15; while in Fig. 1 the section, being slightly oblique, did not pass through a tooth on the left side. The figures in compartment A represent sections through the anterior tooth, in B through the middle tooth, and in C through the posterior tooth. In all cases the sections are arranged consecutively, Fig. 1 being the most anterior, and Fig. 15 the most posterior section; but many sections are omitted. The sections figured were selected because they were in the best condition, and because they were suited to show the form and structure of the various parts of the teeth. All the teeth are shown in the natural position, with their apices directed downwards, but of course with their inner sides far more closely approximated than in the natural condition. The drawings were made from Dr. Parker's consecutive sections. All these figures are magnified 14·5 diameters. The references are as follows in all the 15 figures.

e. p. Oral epithelium. *d. p.* Process of the epithelium passing towards the enamel organ and perhaps the remnant of the neck, which at an earlier date connected the latter with the oral epithelium. On the other hand there are gland-tubes in close proximity, and many appearances render it probable that these may be connected with it. It is seen in sections of the anterior tooth. 1. Inner layer of enamel organ, the columnar enamel cells, and the stratum intermedium of Hannover. 2. Middle layer of enamel organ. 3. Outer layer of enamel organ. *D.* Dentine, coloured red in all the figures in which it is present. *E.* Enamel, indicated as a white line external to the dentine.

P. Tooth papilla. *o.* Layer of odontoblasts. *i. c.* Inner chief cusp. *o. c.* Smaller outer cusp. *N.* Epithelial nodule in the middle layer of the enamel organ, almost immediately over the chief cusps of the two posterior teeth. The references have not been unnecessarily repeated on all the figures.

A—

Fig. 1.—This was the first section in which teeth appeared, and here only on the right side. The shape is long and narrow, and the apex is nearly in contact with the lower surface of the oral epithelium. The direction of the tooth is obliquely downwards and inwards. The dentine is thick, and a thin layer of enamel is present: the former is cut tangentially towards the base of the tooth, and therefore it appears irregularly interrupted by the tissue of the papilla and odontoblasts.

Fig. 2 represents the condition of the next, the second section. The anterior tooth is now seen on the left side, and much resembles the section just described, except that the papilla is only fairly reached at the apex of the tooth. On the right side the tooth is broader, and indicates a tendency towards the formation of two cusps. The entrance of the papilla is seen, although the outer layer of the enamel organ crosses this part of the section at a different level, and can be seen by focussing. Much of the dentine is cut tangentially. The very complete investment of the papilla by dentine is noteworthy, especially when compared with the two posterior teeth. In this and the next figure the dentine is seen to be formed round the very base of the tooth, so that the entering papilla is encircled by it.

Fig. 3 represents the third section; the existence of two cusps seems especially clear on the right tooth. The fourth section is not figured: on the right side the epithelial process (*d. p.*) and the tangentially cut enamel organ are all that can be seen; on the left side the base of the tooth is cut tangentially. The fifth and sixth sections only show the diminishing epithelial process on both sides. The seventh and eighth sections show the tangentially cut enamel organ of the second tooth.

B—

Fig. 4 represents the appearance in the ninth section from the most anterior in which a tooth was seen. The dentine is cut tangentially towards the base on both sides, the apex represents one of the chief inner cusps; on the left side this is cut through at its highest point, and on the right side very nearly so. An epithelial nodule (*N.*) is seen in section above the apex; it may be connected with the inner layer of the enamel organ above the summit of the tooth. A thin layer of enamel is present.

Fig. 5.—The tenth section: the shape of the large inner cusps is well seen on both sides. The layer of odontoblasts (*o.*) is distinct. The small outer cusps are indicated by the direction of the inner layer of the enamel organ (1) on the outer side of the papilla (*P.*). In this vertical section the anterior part of both eyes are also cut through for the first time, and it is thus seen

that the section is very nearly at right angles to the long axis of the head, but a little further posterior on the left side, as is also indicated by comparison of this figure with the last.

Fig. 6.—The eleventh section. On the right side the entrance of the papilla is seen, although discontinuous in this section from the rest of the papilla. On the left side the entrance is seen, and the outer layer of the enamel organ at a different level. In this latter section the small outer cusp (*o. c.*) is shown; no dentine is developed upon it. The large inner cusp is cut through on its posterior slope in the left tooth, and higher up on the slope near the apex in the right tooth.

Fig. 7.—The twelfth section. The two teeth are very uniform, the small outer cusp being seen in both, and the large inner cusp cut low down on its posterior slope. The entrance of the papilla is also distinct. The dentine is cut somewhat obliquely, as in the left tooth of the previous figure. The thirteenth section is not figured; it is incomplete on the left side, so that the tooth is absent; while on the right the tooth is similar to that of Fig. 7, except that the inner cusp is cut at a still lower level.

Fig. 8.—The fourteenth section. The entrance of the papilla is seen to have shifted towards the inner side of the base of the teeth; the inner cusp is now cut through close to its base, while most of its contour is concealed by the enamel organ. An outer cusp is seen in this and in all the remaining sections of this tooth.

Fig. 9.—The fifteenth section. The teeth are now seen in section between the two inner cusps, and no dentine is formed upon any part of the surface. The contour of the enamel organ and oral epithelium on the left side could not be completed.

Fig. 10.—The sixteenth section. In both teeth the anterior slope of the second or posterior large inner cusp can be dimly seen beneath the enamel organ.

Fig. 11.—The seventeenth section. The large cusps are now cut vertically through their apices in both teeth; above the apices the epithelial nodule is seen on both sides (*N.*). In the eighteenth section, not figured, the posterior cusps are cut through on their posterior slopes, rather below the apices. In the nineteenth section traces of the posterior margin of the teeth is seen, and in the twentieth section either the extreme posterior margin of these teeth or the extreme anterior margin of the third teeth.

These sections through the middle tooth (B) should be compared with the surface view of the corresponding tooth in the lower jaw (Fig. 16, B), bearing in mind that the large cusps are external in the latter. Except for this difference, the sections indicate a great general resemblance between the teeth. The number of sections in which a small outer cusp is seen proves that there must be four or five of these structures corresponding to the appearance of the inner side of the posterior tooth (C), shown in Fig. 16.

C—

FIG. 12.—The twenty-first section. The figure indicates that the section passes through the apex of the large anterior inner cusps on both sides. This, together with many previous figures, proves that the anterior slope of the large cusps is much steeper than their posterior slope, for many of the latter are seen in the sections, while at the first, or at most the second section through the anterior slope the apex of the cusp is reached. On the right side the papilla is not continuous. The small outer cusp is seen on both sides in its special compartment of the enamel organ, and the entrance of the papilla is shown in both. These inner cusps are much smaller than those of the second tooth (B), and their dentine is not nearly so thick, and the enamel is very thin indeed and is not represented in the figures. The twenty-second section is incomplete, so that neither of the teeth can be seen.

FIGS. 13 and 14.—The twenty-third and twenty-fourth sections. These show the appearance of the posterior slope of the large inner cusps cut through at two levels; the small outer cusps are very distinct in both.

FIG. 15.—The twenty-fifth section, the last figure. The posterior inner cusp is faintly seen through the enamel organ. The section passes between the two large inner cusps (as in Fig. 9 for the second tooth), but the anterior slope of the posterior cusps are seen from the surface. These are not covered with dentine (compare the posterior outer cusp of the corresponding tooth in the lower jaw, Fig. 16, C, from which dentine is also absent). In the five remaining sections (twenty-sixth to thirtieth) in which traces of the teeth appear, the posterior parts of the last teeth are seen; but nothing is gained by figuring them. The twenty-ninth is the last section in which the eyes appear. It is clear that the third tooth is considerably smaller than the second (compare Fig. 16).

FIG. 16.—× 9. Two teeth in the lower jaw, corresponding to the second and third (B and C) upper teeth, shown in the above-described sections. The piece of jaw from which the preparation was made ended abruptly anteriorly (in the direction of the arrow), so that the presence of an anterior tooth (corresponding to A in the sections) could not be ascertained. However, some sections of the opposite inferior maxilla render it probable, although not certain, that the tooth is present. The superficial structures (epithelium, mucosa, and enamel organ) were dissected away so as to expose the upper surface of the teeth. The inner side of the anterior tooth (B) had been previously cut so that all the inner cusps, except the anterior one, are removed, and the tooth papilla, enamel organ, and sub-epithelial tissues are seen in section. The enamel organ was easily removed from the surface of the teeth, except at the upper parts of the calcified cusps to which it strongly adhered, doubtless due to the formation of enamel in this region, and the consequent adherence of the inner layer of the enamel organ. The teeth are drawn from above, and from the inner side. The anterior tooth (B) is much the larger. Its large outer cusps (*a. o. c.* and *p. o. c.*) are calcified and hard over the region indicated by

the red colouring, the calcification terminating below in a sharp line of demarcation rendered especially distinct from the fact that the jaw had been faintly stained as a whole in carmine. The tooth is seen in vertical section at *P.*, the reference mark being placed upon the entrance of the tooth papilla. The enamel organ and sub-epithelial tissues are also seen in vertical section at e'. o'. and s'. m'. respectively, and the same tissues are also seen in horizontal section at *e. o.* and *s. m.* The line *l* indicates the boundary between enamel organ and sub-epithelial tissue. Between the two teeth (B and C) at the point *x.* the two enamel organs appear to become fused. I could not, however, feel sure upon this point. The entire crown of the smaller posterior tooth is shown, and it is seen that there are four small inner cusps (the reference being to the anterior one) besides a very minute fifth cusp. The large anterior outer cusp (*a. o. c.*) is calcified, but the smaller posterior outer cusp (*p. o. c.*) remains soft like the inner cusps. Part of the inferior maxilla is shown at *B.* The appearance of these teeth strongly confirms the conclusions as to relative size, shape, and structure, drawn from the sections of corresponding teeth in the upper jaw (Figs. 4—15). The relative position of the large and small cusps on the upper and lower teeth respectively is an obvious remnant of the time when the surfaces of the upper and lower teeth fitted together for the performance of mastication.

PLATE III.

Fig. 1.—× 188. A portion of a vertical section through one of the developing teeth of Ornithorhynchus. The tissue had not been decalcified, and hence the structure of dentine and enamel is better shown than in other cases. The teeth of which the structure is shown were contained in an isolated piece of tissue, probably removed from the lower jaw. The relative position of the tooth from which the section was taken is uncertain, but the histological details are evidently quite typical. *m. m.* The middle membrane of the enamel organ, made up of a honey-combed reticulum of cell-plates. Capillaries are present in it, but could not be seen in the part of the section figured. *s. i.* Stratum intermedium of Hannover: the outlines of the small spherical cells are not indicated. *e. c.* The enamel cells: long and columnar, bounded by a sharp and almost straight line of demarcation from the last-mentioned layer, and separated by a very irregular line from the enamel prisms. *E.* The enamel prisms: the layer is faintly marked by fine closely placed lines, running parallel to the surface. The axes of enamel prisms are seen to form an obtuse angle with the axes of the enamel cells, perhaps due to shrinkage. I could not determine whether each prism exactly corresponds to an enamel cell, although this is probably the case. The prisms are faintly stained round the projections of the last-mentioned layer, probably due to incomplete

calcification. *D.* The dentine: probably entirely typical, for the fact that the number of tubules appears to be smaller than usual doubtless follows from methods of preparation or preservation. The dentinal fibres are seen in Fig. 2 to be very numerous. The faint oblique striation in certain parts is probably due to parallel cracks in the brittle calcified tissue when cut by the razor. The black spots represent the uncalcified "interglobular spaces," *D′*. The inner part of the dentine which stains deeply, probably on account of its recent formation. The boundary between this and the completely formed dentine (*D.*) is highly irregular, the outer margin of recently formed tissue being reticulate. In mammalian teeth of a similar degree of development this line of demarcation is usually parallel with the inner and outer surfaces of the dentine, and the younger tissue stains less deeply than the older. *o.* The layer of odontoblasts: the appearance is entirely normal. I could not determine whether the dentinal fibres arise from the superficial or from the deeper cells. *P.* The tooth papilla of normal structure and appearance, containing capillaries at *c.*

Fig. 2.—× 405. A small part of a vertical section through one of the lower teeth of uncertain position. In this case the tissue had been decalcified in dilute nitric acid, the thin layer of dentine (*D.*) is stained equally deeply throughout and exhibits no trace of dentinal tubes. The fact that such tubes exist in normal number is, however, conclusively proved by the numerous dentinal fibres (*o.f.*) which have been drawn out of them, doubtless because of the shrinkage of the internal softer tissues. The fact that some of these fibres (*o′.f′.*) are much longer than the thickness of the dentine must be due to the stretching of the former to far beyond their normal length, probably because their distal ends remained fixed in the dentine during the process of contraction. Each fibre appears to arise from the apex of a minute conical process, projecting from the surface of the layer of odontoblasts (*o.*). This appears to support the opinion that the fibres are at any rate in many cases derived from the superficial cells. The tissue of the papilla is seen at *P.*

Fig. 3.—× 188. Transverse sections of the enamel prisms, seen in a section from the same tissue as that from which Fig. 1 was taken. The shape is seen to be irregularly polyhedral; but the variations in this respect and in size are considerable. The irregularity in size is further proved by the fact that the prisms drawn in Fig. 1 appear to be much more slender than those which are here represented.

Fig. 4.—× 188. A vertical section through a portion of the upper surface of the enamel organ, viz. the surface which is nearest to the oral epithelium. The figure was drawn from one of Dr. Parker's sections of the posterior upper tooth on the right side. The whole tooth is shown (× 14·5) in Fig. 14 on Plate II. The mucosa forming the tooth-sac is represented at *m.*, and the highly irregular outer membrane of the enamel organ at *o. m.*; the cell-outlines are not indicated. The middle membrane of the enamel

organ is seen at *m. m.* It is of normal structure, except that it certainly contains abundant blood-vessels. The vascularity of the enamel organ has been frequently affirmed and denied by various observers, but there can be no doubt about the question in Ornithorhynchus. A normal capillary is seen in the tooth-sac at *c.*, and it can be traced deeply into the "stellate reticulum" of the enamel organ at *c'.*, accompanied by a small amount of connective tissue (*m'.*) from the tooth-sac. The appearance of the deep section of the blood-vessel is somewhat peculiar, but continuity with an undoubted capillary outside the organ, in this and in many other cases, leaves no doubt as to the true nature. It is possible that the appearance of a thick-walled or even solid cylinder of fusiform cells may be due to the shrinkage of a relatively large thin-walled vascular channel, following from the peculiarly delicate and fluid condition of the surrounding tissues. The absence of this latter cause may account for the fact that the external capillary at *c.* and the capillaries in the tooth papilla (Fig. 1, *c*) possess an entirely normal structure and appearance.

Fig. 5.—× 188. A portion of a section of the middle membrane of the enamel organ, showing the structure of its deeper part close to the stratum intermedium. The section was taken from the same tissue as that from which Fig. 1 was drawn. The figure indicates that the vascular channels (*c'.*) penetrate the layer to a great depth, carrying a small amount of connective tissue (*m'.*) with them. The structure of the channel resembles that of the deeper part of the blood-vessel, described in the last figure (*c'.*). An apparent lumen is shown at *l.* It is probable that the vessels shown in this and the last figure are the main vascular channels, and that smaller branches form a network in the middle membrane of the enamel organ. Such a conclusion was suggested by many of the sections.

Fig. 6.—× 188. From the same tissue as the last section, showing the structure of the epithelial nodule in the most superficial part of the middle membrane of the enamel organ, immediately over the apex of each chief cusp of the large broad posterior teeth. The relative position of cusp, nodule and oral epithelium is shown in many of the figures in Pl. II. The nodule (*N.*) is seen to lie in the superficial part of the middle membrane of the enamel organ (*m. m.*), and immediately below the irregular and apparently discontinuous outer membrane (*o. m.*). The tooth-sac is seen at *m.* A space (*c. sp.*) in the middle membrane probably contained a vascular channel. The nodule is seen to be made up of a dense outer tissue, composed of fusiform deeply-staining cells surrounding a concentric space, in which are scattered thin yellowish cells, with a central dense mass made up of similar cells. The latter are not indicated by outlines, but by the presence of minute traces of a nucleus. In some sections an obliquely-cut cylinder of similar structure appears to extend from the nodule towards the apex of the cusp, and is perhaps continuous with the inner layer of the enamel organ or the stratum intermedium in this locality.

Fig. 7.—× 50. A section from the same lower jaw as that from which Fig. 2 was drawn. Behind and interior to the comparatively highly-developed posterior tooth there was a much earlier rudiment of a third or fourth tooth, also present in the upper jaw. The whole appearance exactly resembles the corresponding stage in the development of teeth in the higher mammalia. The oral epithelium is shown at *e. p.* Beneath this the young enamel organ is also coloured red, and its constituent layers are diagrammatically represented. The enamel cells (*e. c.*) of its inner layer are of the normal columnar type; externally to these the very thick stratum intermedium (*s. i.*) is shown, and then again the beginning of a middle membrane at *m. m.*, covered by an outer membrane (*o. m.*) of cells which have already lost their primitively typical columnar shape and have become somewhat flattened. The tooth-sac (*s.*) is clearly marked off from the surrounding mucosa and submucosa (*m.*), and continuous with it is the well-marked tooth papilla (*P.*), which ascends into the space formed by the invagination of the enamel organ. The "neck" of the enamel organ is not seen in the figure; it is continuous with the oral epithelium.

PLATE IV.

Fig. 1.—Natural size. The right side of upper bill and palate seen from below, showing the relative position and form of the horny plates. The longitudinal ridge of the anterior plate is nearer to its outer margin, and between it and the inner margin there is a shallow furrow. The three concave surfaces of the posterior plate are plainly seen. The animal had not attained the full size, so that both plates are smaller than usual, or perhaps the smaller size may be due to sex. Anteriorly, in the middle line, is an oblique furrow containing a canal which leads to the nasal passages, and on the inner side of its opening into the furrow a small but distinct tubercle is seen. Posterior to this are many curved corneous ridges.

Fig. 2.—Natural size. *A.* The socket of the right upper posterior plate, seen from below. The concavity of the alveolus is seen to very roughly correspond to the two posterior concavities of the plate, while it possesses a small but distinct and well-separated anterior and internal compartment for the corresponding concavity of the plate. The bony wall is very thin over most of the alveolar surface, and it is seen to be perforated by numerous foramina through which vessels, &c., pass to the base of the horny plate. *B.* The surface of the right upper posterior horny plate as seen from below. The internal border is very thick, and reaches a much higher level than any other part; and the anterior and posterior borders are much lower than the others. The small anterior and internal concavity is at a somewhat lower level, and

is excavated to a much greater depth than the others. The divisions between the compartments are lower than the borders of the plate.

Fig. 3.—Natural size. *A.* The socket of the right lower posterior plate, seen from above. The concavity is in this case somewhat distinctly compartmented to correspond with the two chief parts of the plate. Each compartment is roughly divided into four small concavities. There is also a very distinct posterior and internal small compartment for the corresponding part of the plate. The bone is pierced by numerous foramina, leading into the very large canal for the inferior dental nerve. *B.* The surface of the right lower posterior horny plate, as seen from above. The outer border is here thicker and somewhat higher than the inner, but the highest part is the anterior border, and especially its inner part; the posterior border is also higher than the lateral borders. The third small concavity is here posterior in position, and it is not excavated so deeply as the others, and its edge is somewhat higher than the adjacent borders. The divisions between the compartments are lower than the borders of the plate. A comparison of the relative heights of the borders and other parts of these plates will show that they are very well adapted for interlocking in mastication, an antero-posterior motion being especially favoured.

Fig. 4.—× 24·5. A transverse vertical section through the left upper anterior horny plate. The section was taken towards the posterior end at the maximum breadth of the plate. The ridge and furrow are seen in section. The structure is obviously entirely epithelial, and passes into the oral epithelium on both sides. The section was cut and stained, and the stratum Malpighii is clearly shown in the lower part, and the stratum corneum in the upper. Numerous fine papillæ enter the former, and each of them sends up from its summit a long column of soft, deeply-staining cells into the stratum corneum. These columns reach the surface, and doubtless largely determine the relative wear of the plate. Thus they are absent or very minute in the ridge, and especially large in the furrow.

Fig. 5.—× 9. A similar section through one of the upper posterior plates; the slight elevation in the concavity being doubtless an oblique section of the low ridge which separates the two concavities. This section had been ground down and dried, so that the papillæ and columns of cells have dried up, their place being occupied by air which causes the dark appearance. The raised borders have only very minute papillæ, &c., in some places. The continuity with the oral epithelium is also seen.

Fig. 6.—× 24·5. A horizontal section through the stratum corneum of the plate shown in Fig. 4. The section was cut and stained, and shows the columns of soft cells in transverse section. The position of the ridge and the furrow can be determined by the size of the columns.

Fig. 7.—× 50. A horizontal section through the stratum corneum of the concavity of the plate shown in Fig. 5. The section was cut and stained,

and shows that the columns of soft cells occur isolated, and also arranged in small groups. The concentric arrangement of cells round the columns is indicated, and the corneous cells which make up the hard part of the structure are represented by their darker central portions (better shown in the next figure).

Fig. 8.—× 405. A single column of moderate size from the inner part of the section drawn in Fig. 6. The column is seen in transverse section surrounded by concentric cells, and these again by the matrix of corneous cells. The column itself has stained deeply, especially the central cell, while the concentric cells stain faintly and the corneous cells remain unstained. Each of the latter contains a central mass of granular appearance, and containing minute pigment granules. It probably represents the remains of the nucleus, together with some of the granular material which occupies a much larger space in many softer cells (compare the concentric cells of this section and various cells in Fig. 11). This central portion remains comparatively soft and dries up in ground sections, being replaced by air.

Fig. 9.—× 188. A horizontal section through the stratum corneum of the concavity of one of the posterior horny plates. The section was ground down, dried, and mounted in balsam, and the latter medium has displaced the air from most of the larger spaces caused by the shrinkage of the columns and the majority of concentric cells. Some of these latter, however, retain abundant air and appear dark, and the same is true of the centres of the corneous cells. In other cases the air may remain in the shrunken columns, so that the resemblance to the Haversian systems of bone would be even more striking than in the figure.

Fig. 10.—× 188. A part of Fig. 4, more highly magnified. The figure represents a vertical section through the superficial stratum corneum of the outer slope of the plate. Two columns of soft cells are seen rising to the surface through the matrix of corneous cells.

Fig. 11.—× 188. A vertical section through the lower part of one of the posterior upper plates, including the bone. The space between the plate and the bone is seen to be very narrow, when the magnification is taken into account. This appeared to be the case in all the sections of the posterior plates. One of the long thin papillæ is seen together with the base of another. The stratum Malpighii is of normal appearance: at its upper part the cells become granular, and higher still become corneous peripherally. Above this we enter the stratum corneum, where the cells are more flattened and become almost entirely cornified. Nevertheless many cells occur, especially in the lower part of this layer, in which the thickened border is alone corneous, while the central part remains granular and is coloured by carmine. At a higher level than that shown in the figure the nucleus ceases to be distinct, but a central granular pigmented mass remains (compare Fig. 8). The soft cells of the column which rises from the apex of the papillæ

are generally granular, although many of them retain the characters of the cells of the deeper layers of the rete Malpighii.

Fig. 12.—× 405. A vertical section through a few granular cells which are becoming corneous peripherally.

Fig. 13.—× 50. A transverse vertical section through the oral epithelium of the right side anterior to the upper true teeth in the young animal. The section was the seventh in front of the most anterior which contained teeth, viz. that which is figured in Plate II, Fig. 1. The thickened epithelial ridge, which perhaps represents the anterior part of the posterior horny plates, is shown in section.

A

Fig. 1.

× 14.5

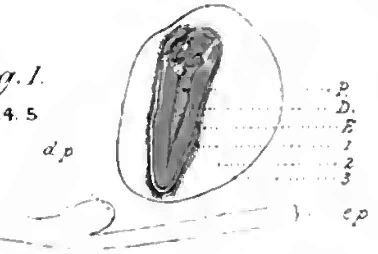


Fig. 2.

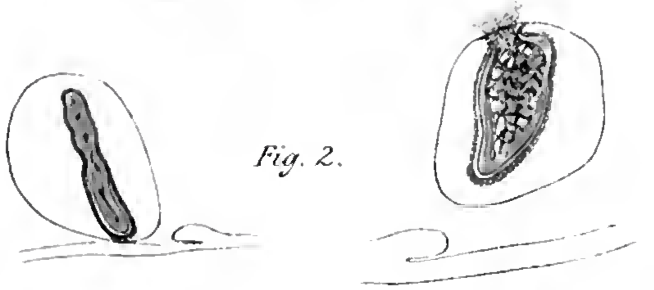
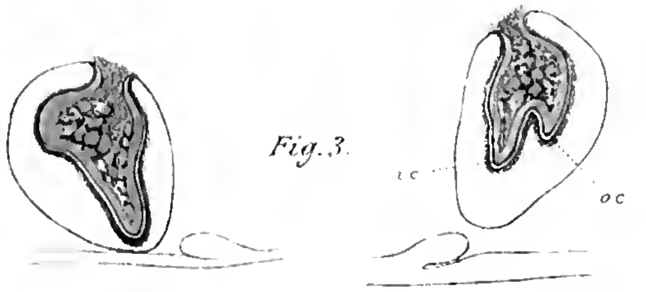


Fig. 3.



B

Fig. 4.

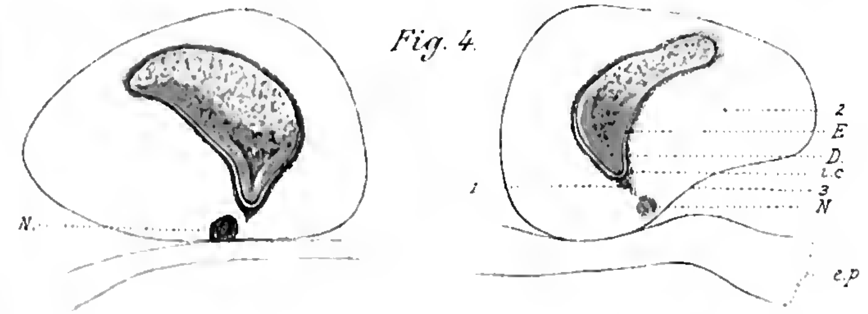


Fig. 5.

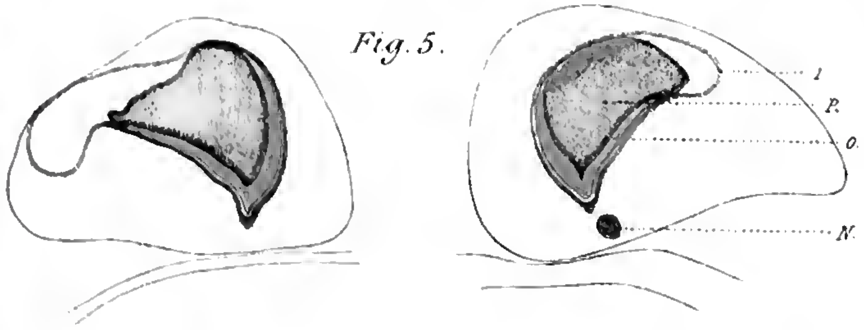


Fig. 6.

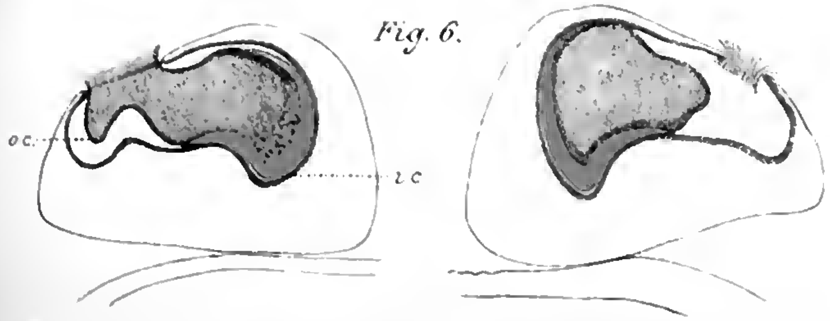


Fig. 7.

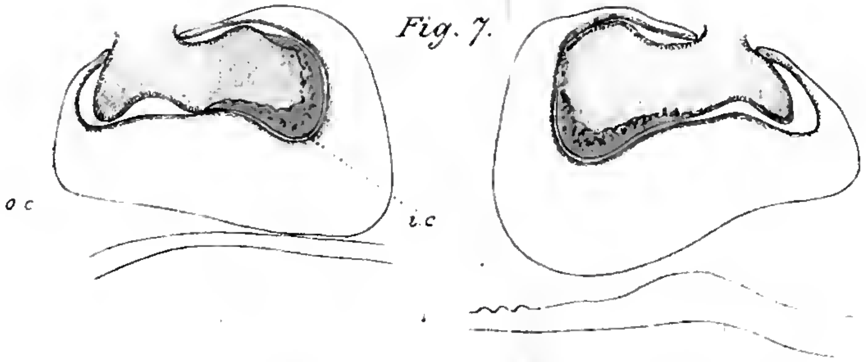


Fig. 8.

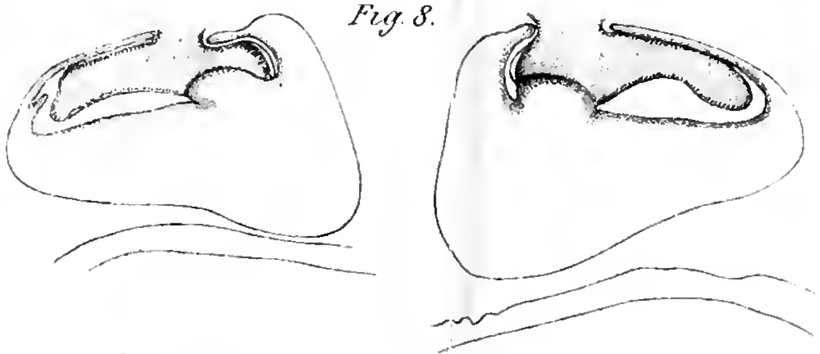


Fig. 9.

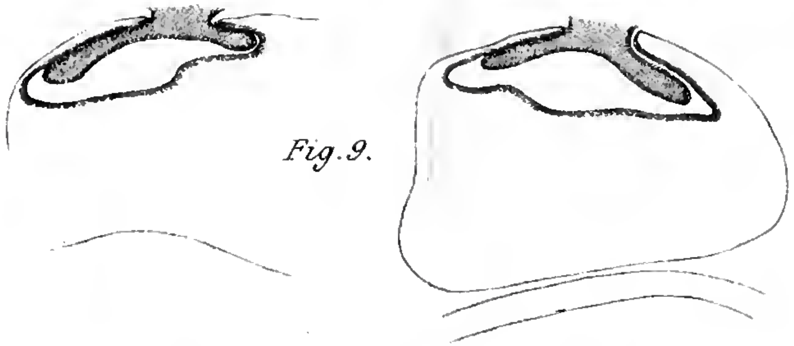


Fig. 10.

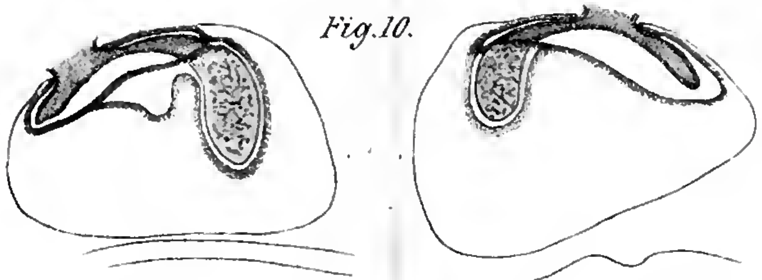
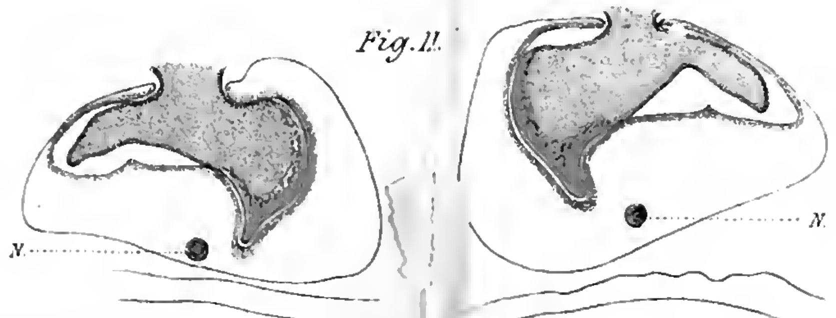


Fig. 11.



C

Fig. 12.

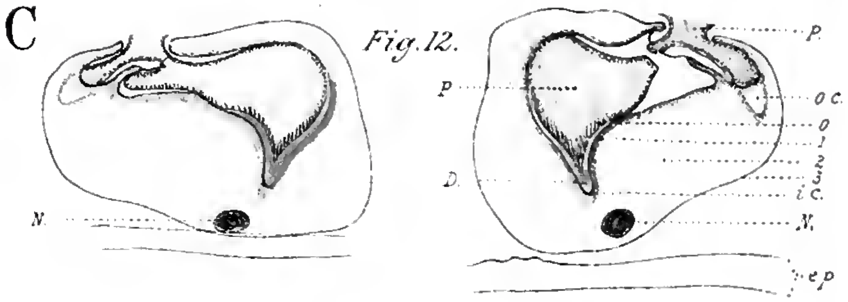


Fig. 13.

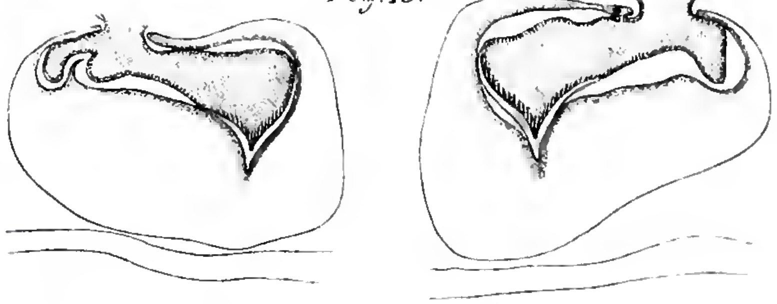


Fig. 14.

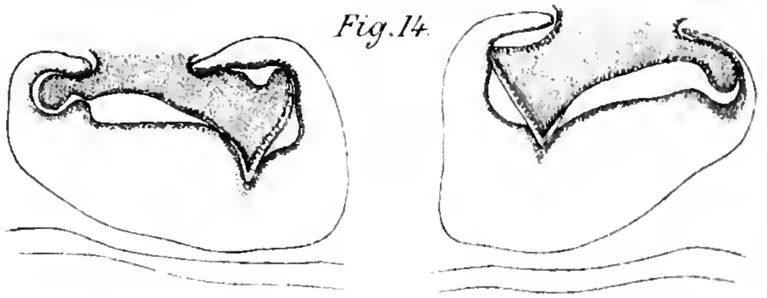


Fig. 15.

× 14.5

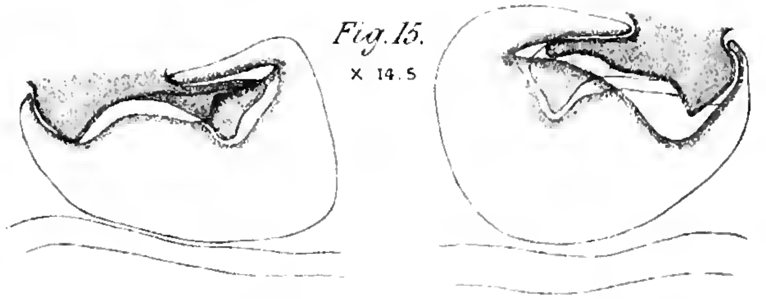
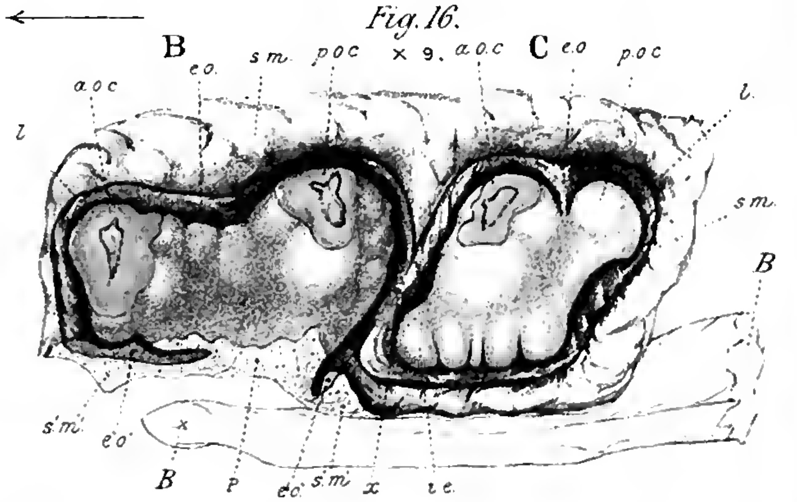


Fig. 16.



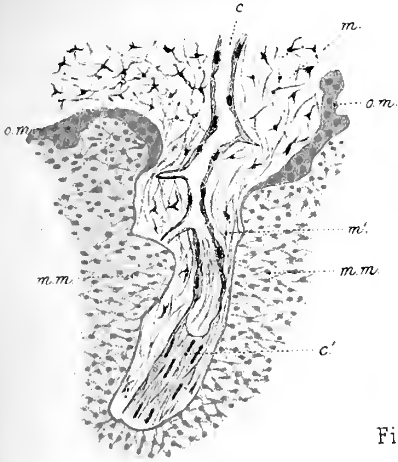


Fig. 4 x 188

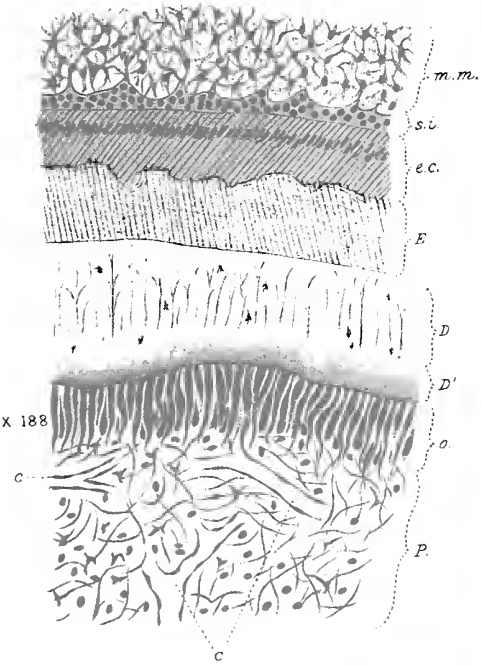


Fig. 1 x 188

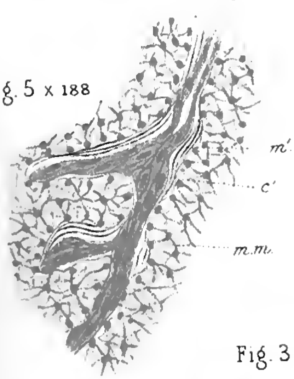


Fig. 5 x 188

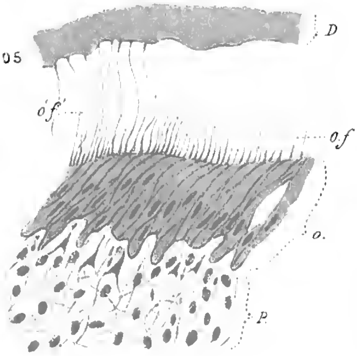


Fig. 2 x 405

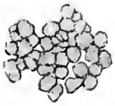


Fig. 3 x 188

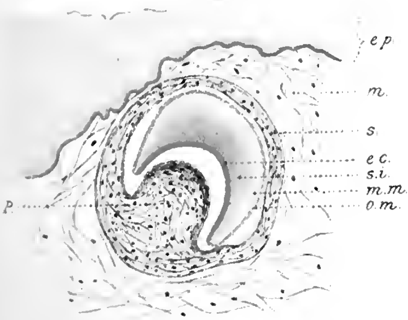


Fig. 7 x 50

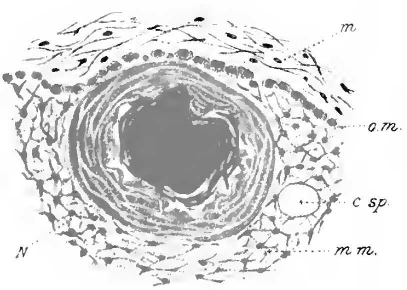


Fig. 6 x 188

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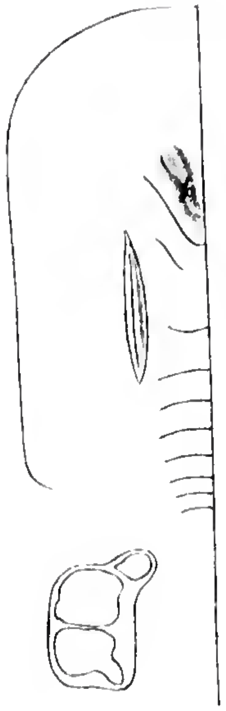
Fig. 1 n.s.


Fig. 2 n.s.

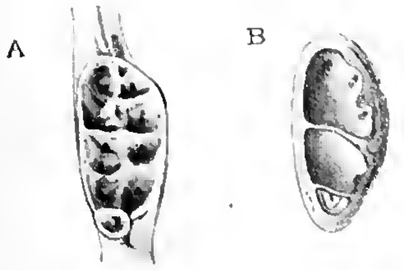
Fig. 3 n.s.

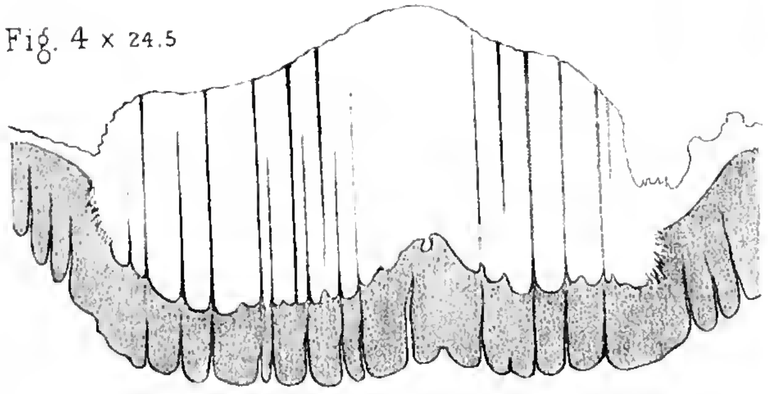
Fig. 4 × 24.5

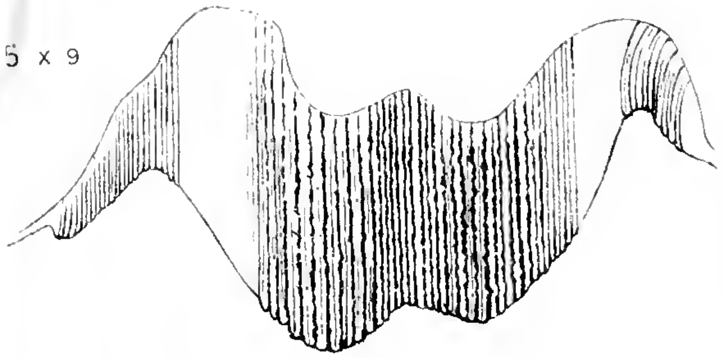
Fig. 5 × 9

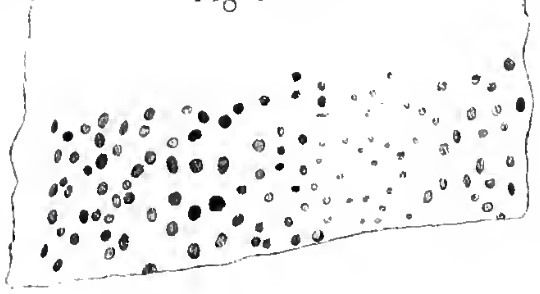
Fig. 6 × 24.5

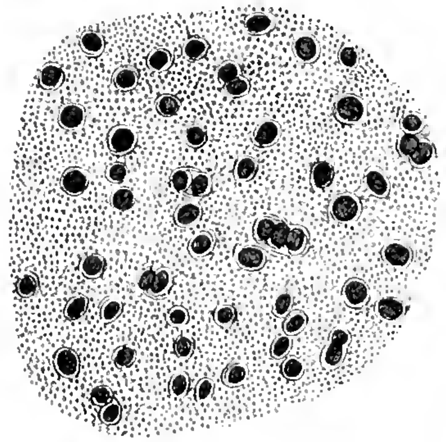
Fig. 7 × 50

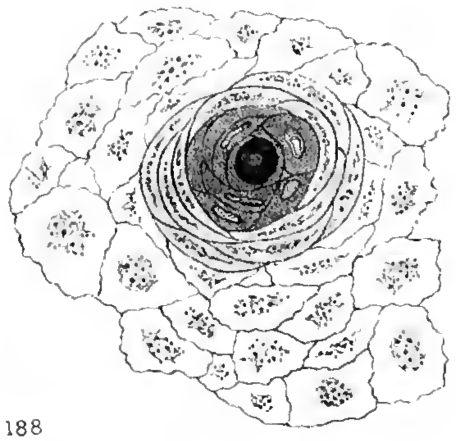
Fig. 8 × 405

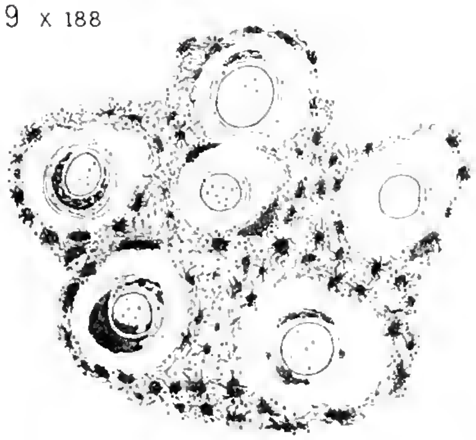
Fig. 9 × 188

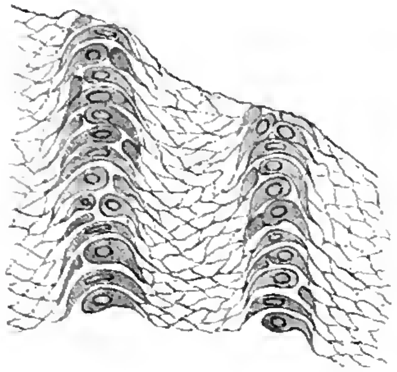
Fig. 10 × 188

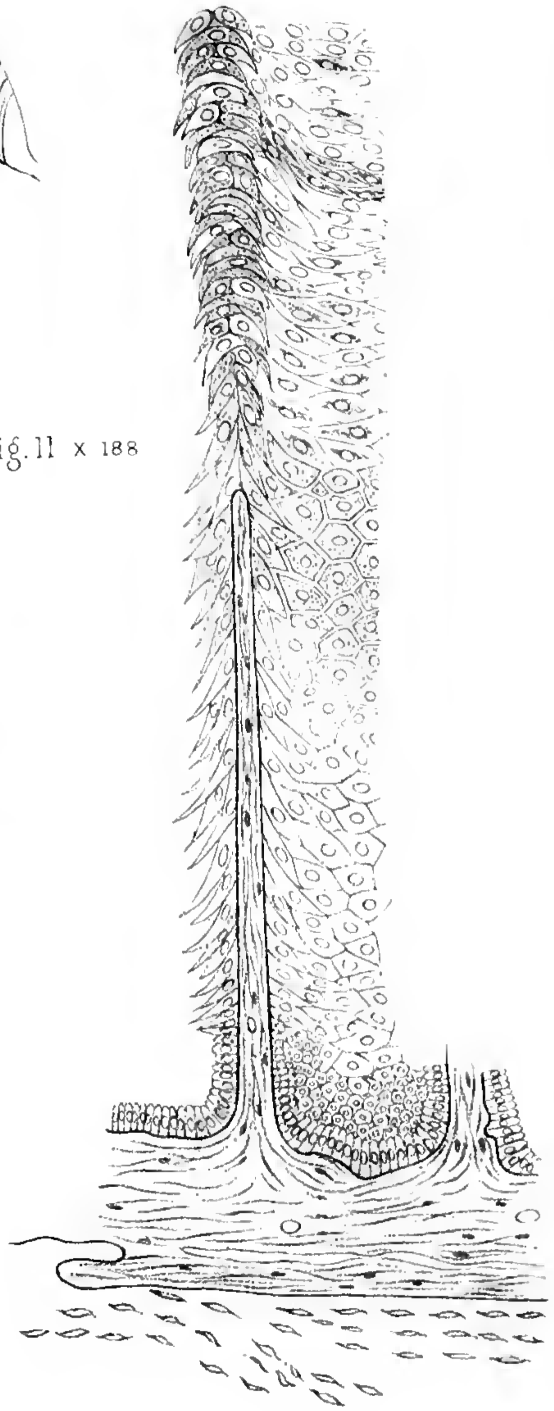
Fig. 11 × 188

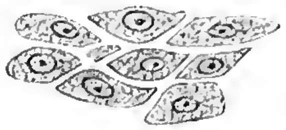
Fig. 12 × 405


Fig. 13 × 50

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Note on the Fate of the Blastopore in Rana temporaria.

By

Harold Sidebotham, M.R.C.S.

With Plate V.

In the description given in Balfour's 'Comparative Embryology' of the development of the Amphibia, that portion of it which specially relates to the anourous Amphibia is mainly founded on the researches of Götte on Bombinator. It is there stated that[1] "at first the mesenteron freely communicates with the exterior by the opening of the blastopore. The lips of the blastopore gradually approximate, and form a passage, on the dorsal side of which the neural tube opens . . . . The external opening of this passage finally becomes obliterated, and the passage itself is left as a narrow diverticulum, leading from the hind end of the mesenteron into the neural canal. It forms the post-anal gut and gradually narrows, and finally atrophies. At its front border, on the ventral side, there may be seen a slight ventrally directed diverticulum of the alimentary tract, which first becomes visible at a somewhat earlier stage. This diverticulum becomes longer and meets an invagination of the skin, which arises in Rana temporaria at a somewhat earlier period than represented by Götte for Bombinator. This epiblastic invagination is the proctodæum, and an anal perforation eventually appears at its upper extremity."

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[1] Balfour, 'Comp. Embryology,' 2nd edit., vol. ii, p. 130.

In a paper[1] "On some Points in the Early Development of Rana temporaria" Professor Spencer states that he is unable to find any trace of the inclusion of the blastopore by the neural folds, or any trace of the closure of the blastopore itself. He also states that soon after the stage has been reached in which the neural folds have met, the hinder part of the neural tube becomes closed, though the blastopore itself remains open.

Miss Johnson and Miss Sheldon have also published some "Notes on the Development of the Newt,"[2] in which they make some remarks with regard to the Frog. They apparently agree with Professor Spencer in the opinion that the blastopore persists as the permanent anus.

Mr. Herbert Durham[3] has also stated that he fully agrees with Professor Spencer in regard to the fate of the blastopore.

Being interested in this question I have cut a large number of series of sections of Rana temporaria. A careful study of these sections leads me to come forward and express my opinion, and that with some degree of confidence, as more than sixty embryos have been examined, that the history of the blastopore more resembles the account of it given by Balfour than that given by any of the other authors above alluded to.

After the formation of the neural folds, and while they are still widely separated, the mesenteron opens to the exterior by means of the blastopore, which is situated at the extreme posterior end of the embryo. Fig. 1 shows a median, vertical, longitudinal section, taken at this stage; in it can be seen a well-marked diverticulum from the hind end of the mesenteron, dipping down towards a distinct pit in the epiblast below the blastopore and quite separate from it. This is the rectum forming, and advancing to meet a true proctodæal pit. This embryo has three mesoblastic somites. As the neural folds grow up to meet each other they do not enclose the blastopore, but reach as far as its dorsal rim.

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[1] 'Quart. Journ. Micr. Sci.,' vol. xxv, Supplement, 1885, p. 123.

[2] 'Quart. Journ. Micr. Sci.,' vol. xxvi, 1886, p. 573.

[3] 'Quart. Journ. Micr. Sci.,' vol. xxvi, 1886, p. 508.

Fig. 2 shows the next stage in an embryo with five mesoblastic somites. The neural folds have met and form a tube, bending over the posterior end of the embryo, and opening through the dorsal region of the blastopore, which has become narrower and longer. Below the blastopore the proctodæal invagination may be seen to have increased considerably in depth as also has the rectal diverticulum from the mesenteron.

In fig. 3 the same parts can be recognised, but the closure of the blastopore has proceeded further. This stage has six mesoblastic somites. The septum dividing the rectal diverticulum from the proctodæal invagination has become perforate. The section of which fig. 3 is a drawing is not quite in the right plane for showing the neurenteric canal.

Fig. 4 shows the next stage in an embryo with eight mesoblastic somites. The blastopore is completely occluded, and is represented by a column of epiblastic cells (*ep.*) which may be recognised by their containing much pigment. The anus communicates freely with the alimentary canal, and the neurenteric canal is still well marked. There is a slight dilatation of this canal at the junction of its dorsal and ventral limbs, which dilatation is the post-anal vesicle.

In the next stage, with nine mesoblastic somites, represented by fig. 5, the tail has just commenced to bud out. The remnant of the blastopore is represented only by a little heaping together of the epiblast cells, where the blastopore opened to the surface. The neurenteric canal has become occluded, but still can be traced up as a solid rod of cells, representing the post-anal gut, commencing from the normal position. There is a diverticulum from the proctodæum just before it opens to the surface which is the rudiment of the allantoic bladder.

Thus the history differs from that given by Balfour, in that the neural folds do not enclose the blastopore, the closure of the blastopore being effected subsequently to the meeting of the neural folds. My conclusion differs essentially from the description given by Professor Spencer, inasmuch as I find that the anus is not derived from a persistent blastopore, but is formed from an independent proctodæal invagination.

Miss Johnson and Miss Sheldon, writing with reference to the Newt,[1] incline to the conclusion that the tail, as well as the post-anal gut, is a secondary structure developed after the permanent anus. Of course this view would be equally applicable to the same structures in the Frog, if Professor Spencer is correct as to the fate of the blastopore.

But I think that the condition which obtains in the Frog at the stage when the blastopore is still just open represents an extremely primitive condition, for Balfour, in his paragraph with reference to the post-anal gut and neurenteric canal,[2] comes to the conclusion that the neural and alimentary canals must have had a common opening, probably into a dilated vesicle, before going directly to the exterior. This is exactly what is found in the Frog just before the rectal diverticulum becomes perforate.

Professor Spencer only figures one longitudinal section, and this is from a stage subsequent to that in which the closure of the neurenteric canal takes place, a stage, moreover, at which all trace of the blastopore has gone.

During the time the blastopore is open it always runs in a line with the mesenteron and opens posteriorly, while the rectal diverticulum always runs ventrally, and keeps at about the same angle to the mesenteron, even after the tail has become fairly well developed.

In Professor Spencer's fig. 15 the canal, the extremity of which he marks (*an.*) and describes as the blastopore, I think must be the rectal diverticulum, as I find just the same condition as there represented in my sections taken from embryos at a corresponding age.

His figs. 5 and 6 are taken from an earlier stage than his fig. 15, and show just the same features as do mine, but the appearances they present may easily be interpreted in accordance with my view, the opening he marks *bl.* in both figures being the proctodæal invagination. In his fig. 5 the blastopore is

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[1] Loc. cit.

[2] 'Comp. Embryology,' vol. ii, chap. xii.

continued posteriorly from the point *ne*. My figs. 6 and 7 also show this.

Mr. Durham's drawings also are all taken from a later stage, but are not intended to illustrate the history of the blastopore but the fact of there being a neurenteric canal. In the earliest stage which he figures, the rectum is the ventrally inclined diverticulum, and is shown exactly as I find it. The blastopore is occluded previously to this stage.

Only one series out of over sixty has failed to show this history. It was abnormal in other respects than the blastopore, and was probably pathological altogether.

In conclusion, I wish to express my sincere thanks to Professor Milnes Marshall for looking at my specimens, and also for much kind advice in reference to the subject of this paper.

DESCRIPTION OF PLATE V,

Illustrating Mr. Harold Sidebotham's "Note on the Fate of the Blastopore in Rana temporaria."

Reference Letters.

al. Alimentary canal. *all.* Allantois. *bl.* Blastopore. *ep.* Epiblast. *m.* Mesoblast. *n. c.* Neurenteric canal. *not.* Notochord. *n. g.* Neural groove. *p. a. g.* Post-anal gut. *pr.* Proctodæum. *n. c.* Neural canal. *r. d.* Rectal diverticulum. *sp. c.* Spinal cord. *x.* Yolk.

Figs. 1—5.—Median vertical longitudinal sections.

Fig. 1. From an embryo with three mesoblastic somites. The neural groove is still open, except at the anterior end; the blastopore is widely open; and the rectal diverticulum well marked.

Fig. 2. From an embryo with five mesoblastic somites.

Fig. 3. From an embryo with six mesoblastic somites.

Fig. 4. From an embryo with seven mesoblastic somites.

Fig. 5. From an embryo with eight to nine mesoblastic somites.

Figs. 6 and 7.—Transverse sections from an embryo slightly older than Fig. 1.

Fig. 6. Taken along line *a—a* in Fig. 1.

Fig. 7. Taken along line *b—b* in Fig. 1.

Fig. 1.

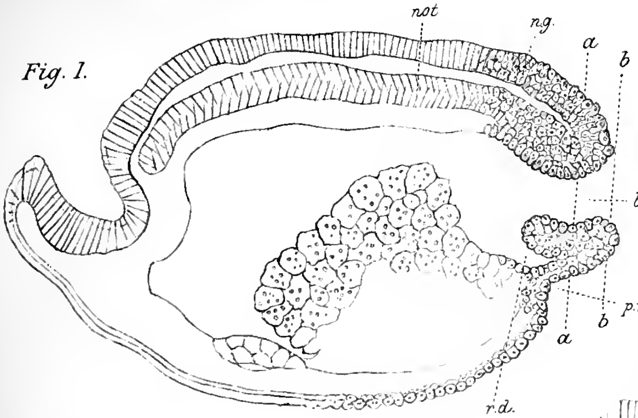


Fig. 6.

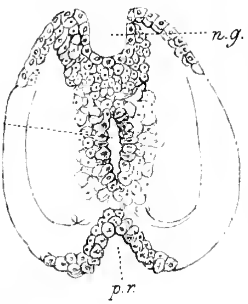


Fig. 2.

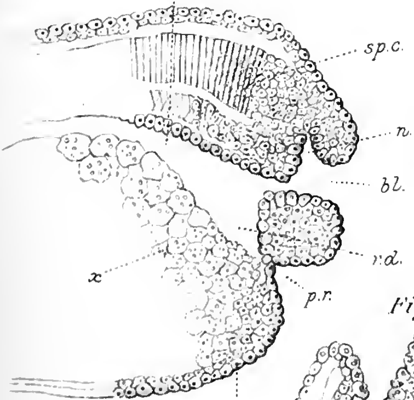


Fig. 3.

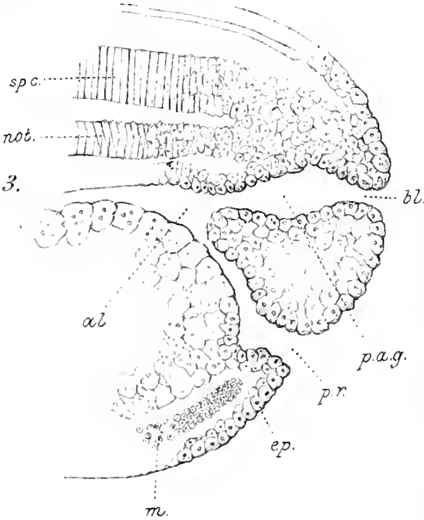


Fig. 7.

Fig. 4.

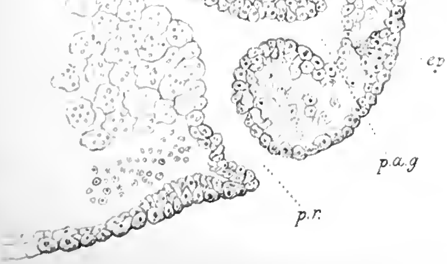
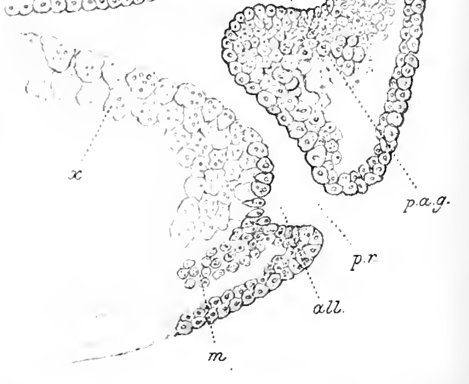


Fig. 5.



H. Sidebothom del
F. Huth, Lith^r Edin^r

Morphological Studies.

No. I.—The Parietal Eye of the Cyclostome Fishes.

By

J. Beard, Ph.D., B.Sc.

With Plates VI and VII.

Introduction.

The discovery of the parietal eye by de Graaf (No. 7), and the beautiful account of its structure in a great many genera of Sauria by Spencer (No. 14) are of so very recent occurrence, and excited so much interest among zoologists, that I can refrain from an historical account of their work and of previous researches on the pineal body, with which this sense organ is identical. Spencer has given a full statement of all that was known of this organ in Lizards, and I shall therefore only preface the following account of its structure in the Cyclostomata by a brief notice of Ahlborn's work on the subject. In his paper on the brain of Ammocœtes Wiedersheim (No. 16) had described the presence of a greyish-white pigment in the pineal body, and this discovery was confirmed by Ahlborn (No. 1, p. 233). Ahlborn has, in addition, given some account of the minute structure of the organ in both Ammocœtes and Petromyzon, and, indeed, as the result of his studies he published in a separate essay (No. 2) some views on the nature of the pineal body—independently of, but identical with, those enumerated by Rabl.-Rückhard (No. 15) some time before.

The circumstances which led both these observers to the hypothesis, afterwards converted into a fact by de Graaf and Spencer, did not favour Ahlborn with the discovery of black pigment in the pineal body of Ammocœtes. Had he chanced to obtain sections such as I figure in figs. 1, 3 and 8 of Pl. VI, there can be little doubt that he would rightly have regarded his idea of the rudimentary eye-nature of the pineal body as more a fact than an hypothesis. I can, from my own researches, easily understand Wiedersheim's failure to find a coloured pigment, black or otherwise, in the pineal body of Ammocœtes, for I have only seen it in the three Ammocœtes to be afterwards described, and such pigment appears to occur very rarely in the parietal eye in the Ammocœtes stage. But for a long time Ahlborn's failure was to me an enigma which I could only explain on the supposition that he had never had fully adult Petromyzon in his hands, for I was fortunate enough to find the black pigment in the first full-grown Petromyzon examined, and it was some time before a Petromyzon in which the pigment was absent came into my hands.

Wiedersheim's and Ahlborn's negative results regarding the presence of black pigment are easily explicable, as will afterwards be seen. Not all Petromyzon, and still less Ammocœtes, possess the black pigment in the parietal eye.

Since Spencer's researches appeared, the only accounts of actual work published on the parietal eye are the preliminary notice of my own discoveries (No. 3, p. 246) and Béraneck's account of its development in Lacerta and Anguis (No. 4).

I shall have occasion further on to refer to Béraneck's paper. Here, be it remarked, that in his account of the development there is little or nothing that was not already known.

I have also worked the development in these two forms, and if I refrain from publishing the results it is only because I agree with another observer, who also has investigated the matter, that there is little or nothing to make known which is not already common knowledge.

The Cyclostomata were chosen for the following research on account of their, in many points, exceedingly primitive characters. I hoped from their investigation to get insight into the phylogeny of the parietal eye, for of that we know nothing. Spencer's otherwise beautiful researches do not appear to throw any reasonable light on the former history of that organ, and the only point about its ancestry that one can accept as the outcome of Spencer's work is his conclusion (No. 14, p. 233) that "the pineal eye may probably be most rightly considered as peculiarly a sense organ of pre-Tertiary periods."

As it was hardly to be expected that the organ had originally developed in the group of Reptiles, the fishes were naturally turned to as affording the most probability of finding the solution of the problems it presents. The result of an examination of the Cyclostomata has been to alter Spencer's statement, true as it was when he wrote it, that "there is not sufficient evidence to prove or disprove the existence of the organ within the group Pisces" (No. 14, p. 233).

In addition to Myxinoid fishes I have examined several Teleostei, among them Callicthys, but with negative results as to the presence of an eye-like structure.

Callicthys was brought under my notice by both Professors Wiedersheim and Howes on account of the curious "parietal foramen" it presents in the median line above the snout, but in front of the brain.

This membranous portion of the skin has, however, nothing to do with the epiphysis; what its meaning is I am unable to say, for I have only investigated its possible relations to a parietal eye. In Myxine, some Ammocœtes, and nearly all adult Petromyzon examined by me the presence of a fairly well-organised parietal eye could be determined.

I begin with the account of the structure of the parietal eye in

The Ammocœtes of Petromyzon planeri.

I have had at my disposal a very large number of Ammocœtes obtained in Freiburg, and near Kirnhalde, in the Schwarzwald. In addition, Herr Schwarz, a pupil of Professor Weismann's, lent me sections of three Ammocœtes, to be described shortly, and he has allowed me to figure them in figs. 3, 5, 6, and 10. The three Ammocœtes of Herr Schwarz probably came from the same brook, and are remarkable when compared with every other Ammocœtes I have examined, in that there is a very deep deposit of black pigment in the parietal eye.

Ahlborn (No. 1, p. 230) has described very correctly the topographical relationships of the pineal body in both Ammocœtes and Petromyzon, and all I need remind the reader of here is that it is in both still connected with the brain, and not pinched off from the pineal stalk, as in Anguis, and that very early in development the pineal body is divided into two vesicles, a dorsal one, the parietal eye, and a more ventrally situated one, which never possesses black pigment, and never presents any resemblance to an eye.

In the following account of the minute structure we are solely concerned with the dorsal vesicle. I shall not describe the structure of the ventral vesicle, which is represented as seen in Petromyzon (longitudinal vertical section), in figs. 8 and 9, *v. v.*

The dorsal vesicle or parietal eye (*P.E.*) lies some distance below the surface of the body and within the skull, which dorsally is only membranous (figs. 3 and 5, Pl. VI).

As pigment is at this period of the animal's life but sparsely scattered in the skin there is not such a marked pigment-free spot above the eye indicating its position, as in Petromyzon.

The eye is almost hemispherical in appearance, and has the anterior wall flattened. The anterior and posterior walls are separated by a narrow space (figs. 3, 5, Pl. VI), which is filled with an albuminous coagulable fluid (fig. 9, *cf.*). The coagulation of this fluid led Ahlborn (No. 1, p. 233) to the conclusion that the cells of the two walls were connected by threads. This is not the case, and Spencer has already suggested the explanation given above (No. 14, p. 222, foot-note).

The anterior wall occupies the position but lacks the structure of a lens, as described by Spencer in Hatteria, &c., and by de Graaf in Anguis. It is, however, thicker in the centre than at the sides (figs. 3, 5, and 10, *l.*), and might perhaps be compared to a slightly convex lens. The only thing that can be made out in its structure is a fairly large number of rounded nuclei lying in a certain amount of protoplasm. Cell boundaries are here not to be made out in the Ammocœtes.

The posterior wall (figs. 3, 5, and 10, *re.*) presents structures which one may compare with a retina, such as that described by Spencer in Hatteria or Varanus (No. 14, p. 177).

This portion is much thicker than the anterior wall, and its widest part is in the middle. It is figured in Schwarz's three specimens (in figs. 3, 5, and 10, *re.*). It presents from within outwards a layer of longish rods (*rd.*), the free ends of which line the cavity of the vesicle. Without the rods is a layer of nuclei (*n.*, figs. 3, 4, and 10), and beyond these a second more scanty layer of scattered nuclei (n^2.)is met with. The rods are elongated cells, whose nuclei lie near their bases. In the three Ammocœtes mentioned the rods are more or less enveloped in a deep black pigment, which extends to their bases, and even slightly into the layer of nuclei beyond. The internal row of nuclei are, like the fewer external nuclei, rounded, and could not be traced into connection with the rods, though probably such connections exist. The protoplasm in which the outer nuclei rest is granular and fibrillar in appearance. Thus the retina of the parietal eye of Ammocœtes presents practically the same structure as that of Hatteria or Varanus figured by Spencer (No. 14, Pl. XIV, figs. 3 and 6). If the reader will compare these figures with my figs. 3, 5, and 10, he will, I think, be convinced of the agreement.

I have previously stated that more usually the parietal eye retina of Ammocœtes presents no pigment. I have figured a longitudinal section (fig. 4) of such an unpigmented parietal eye, and this is typical of most Ammocœtes. While it presents in other respects the same characters as the three specimens described above pigment is very nearly but not quite absent; there are a very few minute dots, which are figured at *p. s.*, fig. 4.

Where the pigment is absent it is not possible in specimens prepared according to the usual methods, viz. sublimate or even chromic-osmic-acetic acid, to make certain of the connection of the rod-like retinal elements with the inner and outer nuclei. As the demonstration of such connection is more the work of the histologist than of the morphologist, and as I am concerned here more with the morphological aspect of the matter, I am content to have shown (1) the presence of black pigment in the parietal eyes of some Ammocœtes, and (2) that the arrangement of the rods and nuclei and cells of the retina of the Ammocœtes parietal eye is essentially that of the same elements in the more perfect organs of Hatteria and Varanus, as described by Spencer.

As in the adult the parietal eye of Ammocœtes is a variable organ—a point which is naturally of importance in connection with the question of its degeneration.

The Parietal Eye in Adult Petromyzon.

In Petromyzon planeri I have been able to make a fairly exhaustive investigation of the organ in question. Petromyzon marinus only came into my hands in the shape of one specimen in a bad condition for histological work. For this specimen, and for an example of Bdellostoma, to be afterwards mentioned, I have to thank Professor Howes.

Externally the position of the organ is marked by a large whitish spot on the skin behind the olfactory hypophysial opening. In Petromyzon marinus it is especially large, and, as in Petromyzon fluviatilis, this spot is due to the absence of black pigment over that portion of the skin. If this white spot is any criterion for the existence of the parietal eye in a fully-developed condition, as I believe is the case, then Petromyzon marinus and Mordacia mordax, as figured by Günther (No. 9, p. 693, fig. 318), must both possess the parietal eye in a fair state of development. The latter form, which is very rare, has not been at my disposal, and owing to the condition of preservation of the specimen of Petromyzon marinus I can give little information of the state of the organ in question. The only two points I could observe were that there is a large white spot, as stated above, and that a deep depression in the cranium just beneath it is readily made out. Now, as this depression in P. fluviatilis is always associated with a fair development of the parietal eye in the individual, I think we run little danger in assuming that the organ will probably be found to be well developed in the marine form, all the more as the marine form is certainly less degenerated than the fresh-water one.

In adult fresh-water Petromyzon one finds the same variation in the presence or absence of pigment which we met with in the Ammocœtes, a fact which partially accounts for the non-finding of black pigment by earlier observers and especially by Ahlborn.

Relatively to the brain the organ in the adult lies further forwards (fig. 1, *P. E.*), and is connected throughout life with the brain by a somewhat long stalk. Its position and relations to the left ganglion habenulæ have been already described by Ahlborn (No. 1, p. 233), and he has also recorded its division as in the Ammocœtes into an upper and a lower vesicle, dorsal and ventral.

As in the Ammocœtes the dorsal one alone concerns us directly, for the ventral vesicle never presents any advance on the development as described in the Ammocœtes.

The parietal eye in the adult usually lies in a deep depression of the skull (figs. 1 and 8, *s. f.*), but if no pigment be present in the eye, that is if the organ be ill developed, as happens in some individuals, the corresponding depression in the skull is also almost or entirely absent (fig. 9). This is a very curious fact. The pigment in the skin (*p. s.*) does not reach over the eye. And in longitudinal vertical section of the head one sees that the pigment stops short (fig. 8), some distance before and behind the organ.

Further, the amount of pigment deposited in the eye varies in different specimens. In some the pigment is so thick as entirely to conceal the structure of the retina (fig. 1, *p.*). In others it is more moderately developed (fig. 8, *p.*), and allows an insight into the structural elements of the retina. In others no traces of pigment are to be found (fig. 9).

This again, as in the Ammocœtes, is an indication of the variability of the organ.

When I here speak of pigment I mean black pigment. Ahlborn, following Wiedersheim's discovery of grey-white pigment in Ammocœtes, found in all his Petromyzon only white pigment (No. 1, p. 233). I do not dispute these discoveries, which appear to me well authenticated. As I have never investigated perfectly fresh Petromyzon or Ammocœtes I have never seen this white pigment, but as Ahlborn always found grey-white pigment and no black, and as in my sections if pigment could be recognised at all it was always black, I think we may safely assume that in all those cases of Petromyzon or Ammocœtes where I have found no pigment, the grey-white pigment of Wiedersheim was originally present, but was dissolved out in the process of preparing the sections.

The front wall of the vesicle in adult Petromyzon is very little different from what we saw in Ammocœtes. It contains no pigment and is usually somewhat folded (figs. 1, 8, and 9). It is composed of long cylindrical cells, and can hardly be said to form a lens.

As in Ammocœtes the cavity of the vesicle is filled by a coagulable fluid (fig. 9, *c.f.*) which in sections is drawn into threads which appear to connect the two walls of the vesicle. Of course the importance which Ahlborn attached to these connections is negatived by their nature.

With low powers the posterior wall of the vesicle or retina is seen to be made up of three layers: an inner layer of rods (fig. 9, *r.*) which also contains the pigment; following this a layer of "nuclei" (fig. 9, n^1.), and outside this a somewhat granular striated layer, which contains a few ganglion-cells (fig. 9, n^2.). Outside of all is the connective-tissue investment of the eye.

The retina as figured in figs. 1, 8, and 9 would be comparable to the retina of Varanus or Hatteria as described by Spencer. However, it is interesting and important to examine such a pigmentless retina of Petromyzon under very high power.

Fig. 7 is taken from exceedingly good sections of such parietal eye, and is drawn under Zeiss's objective F.

The end elements are shown to be of two kinds, comparable as it seems to me to those in the retina of the ordinary eyes. By far the most numerous are the long rods (*rd.*), but in addition and between the latter one finds a few cones (*cn.*). The mode of connection of these end elements with the "nuclear layer" is also figured, as well as their termination in an outer ganglion cell layer ($n^2gl.$).

The Parietal Eye in Myxine.

Although I have examined many Myxine in a better or worse state of preservation, I have only found one in which the structure of the organ in question could be well made out. In fig. 12 I have drawn the general appearance and relationships of the organ as seen in sagittal section under low magnification. The eye is a large flattened organ lying within the skull and connected to the thalemencephalon by a short, thick solid stalk (fig. 12, *st.*). In the specimen under description it contained no pigment, the dark portion of the vesicle in fig. 12 being only the optical appearance of deeply stained nuclei in a thick section. The epiphysis is here undivided into two vesicles, in which respect it differs from the corresponding organ in Petromyzon. Both anterior and posterior walls have practically the same structure, although the posterior wall shows the elements in a slightly better developed condition. A piece of the retina (posterior wall) under high magnification is figured in fig. 11. It shows that the structure is made up of a row of rod-like nucleated cells which taper towards their bases. The tapering bases probably end in some of the cells which form a scanty outer layer to the retina. The nuclei of the rod-cells lie not very far away from the cavity of the vesicle. Through the vesicle a number of longitudinal fibres or striæ pass (fig. 11). One may compare the retina here described to that of Cyclodus as figured by

Spencer (No. 14, Pl. XVI, figs. 18 and 19). It appears to be more degenerate than that of Petromyzon, though bearing in mind the variability of the organ in the latter form we must not shut out the possibility that some Myxine may present a much better developed eye than that under description.

In the one specimen of Bdellostoma at my disposal I could make nothing out of the structure of the organ; however, as the brain of this form very closely resembles that of Myxine, as Johannes Müller[1] first showed, it is not at all unlikely that the resemblance will extend to the structure of the parietal eye. The two forms, Myxine and Bdellostoma, are certainly very closely allied, and in other points of great importance, such as the structure of their teeth, they closely resemble each other and form a contrast to the Petromyzontidæ, which while in some respects less degenerate than the former are in others less primitive.

General Considerations and Conclusions.

It was with the hope of getting at the phylogeny of this remarkable sense organ that I began researches on its development and its distribution in the group of Fishes. But indeed the result was only to find that the development explains very little. It is peculiarly one of those cases in which, as Dohrn so often insists, "nicht Anfangs und Endpunkt das wahre phylogenetische Problem bilden, sondern der unbekannte Weg, der sie verbindet."

Leydig, whose misfortune it was to discover the organ in Reptiles years before the modern perfected methods of research enabled de Graaf and Spencer to convert Rabl-Rückhard's (No. 15) and Ahlborn's theoretical conclusion into proved facts (No. 13, p. 535), has recently made use of his undoubted right to an opinion on the question, and declares his conviction[2] that the organ belongs to the system

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[1] 'Vergleichende Anatomie der Myxinoiden,' p. 176.

[2] From a former (erroneous) discovery of his that the organ in Batrachia is ennervated by the trigeminus. There can be little doubt that this is wrong.

of sense organs of the lateral line, and that it finds a parallel in the luminous organs of certain Fishes described by him (No. 13).

It is with regret that one must insist how impossible this suggestion is, and how little likelihood there is that any zoologist will adopt it.

I should be the last person in the world not to agree that the system of lateral sense organs is a very remarkable one, and one from which the so-called higher sense organs, except the paired eyes, will be proved, if the proof is not to everybody's satisfaction yet complete, to have phylogenetically been derived. And although the parietal eye may present resemblances in its structure to Leydig's luminous organs, in all other respects the proposed homology cannot be maintained; and as soon as one attempts to compare the parietal eye in any way with the lateral sense organs all possibility of their homology vanishes. All the lateral sense organs develop apart from the central system, and in connection with cranial nerves and ganglia; while we have no facts as yet which show that the parietal eye is otherwise than a portion of the central nervous system, in which respect it agrees with the paired eyes.

As things at present are, I see no advantage in a further discussion of this matter, and beg to refer the reader who wishes more light on the relations of the central to the peripheral nervous system to the first part of my work on the latter, which may see the light before this paper.

I may pass over Béraneck's recent paper (No. 4) on the development of the organ in Anguis and Lacerta, seeing that it contains practically no facts of importance which were not already known from de Graaf's and Hoffmann's researches (No. 11). Of the latter, Béraneck appears to have been entirely ignorant, although they cover a good deal of the ground of his paper. Only one statement in Béraneck's work calls for notice, and that is his agreement with Spencer (No. 14) that the lens passes continuously over into the retina in Anguis. From his figures I do not suppose M. Béraneck's specimens were in a very good state of preservation, and I must undoubtedly insist against Spencer and Béraneck that de Graaf (No. 8) was right in his assertions.

In Pl. II, fig. 13, I have given a figure of the eye in longitudinal section; it is taken from an advanced embryo of Anguis, and shows very distinctly that the lens is well marked off from the retina by a sharp line of division. I could, if I chose, give similar sections through adult specimens, showing the same fact.

I should not refer to this apparently trifling circumstance were it not of great importance for some considerations to be developed further on.

Regarding Spencer's speculations on the origin of the parietal eye from the larval Tunicate eye, I think I need say little more than I have already said in my paper in 'Nature' (No. 3, p. 246). It reads: "With Wiedersheim and Carrière I consider that Spencer has placed the eye of the larval Tunicate at the wrong end of the series—if it should come in at all; for, as experience has abundantly shown, it is very easy to compare organs of the higher Vertebrates with what are supposed to be homologous organs in Amphioxus and the Tunicata, and at the same time to be entirely in error. I need hardly refer the reader to the instances in which such comparisons have been shown by Dohrn, in his well-known 'Studien,' to have been entirely wrong." One might suppose the degenerate nature of the Tunicata had been sufficiently proved, and it is impossible to look with any favour on Spencer's attempt to re-establish that group in the position of ancestors of Vertebrates, or, what is practically the same thing, near allies of such ancestors. One thing more: in Spencer's diagrammatic plate (No. 14, Pl. XX), illustrating "the rise and fall" of the parietal eye, he begins with a slight evagination of the brain (larval Tunicate, fig. 1), which shows one layer of cells, whose inner ends, their bases, are evenly pigmented. The next two stages (Pl. XX, figs. II and III, Bufo) the pigment is more confined to the centrally situated cells of the evagination, that is, in those cells which, if the thing developed into a parietal eye like that of Hatteria, would form the lens. This would be inconvenient—very much so. So in Pl. XX, fig. 4 we have a figure of an early stage of a higher chordate, in which the pigment has all disappeared; and when in further development (Pl. XX, figs. 7 and 8, Reptiles) we find it again, it is confined to its proper place in the retina, and the lens contains no pigment; while if it had developed from the structures in figs. I, II, and III —if it could perform the physically impossible task of developing—it would be loaded with pigment. Now, these diagrams are not untrue to nature, and all my criticism aims at proving is that Spencer's arrangement of them is artificial and misleading. It would be a misfortune if these diagrams got into the text-books in the order in which Spencer gives them. Even if placed in a less artificial order they do not show the phylogenetic development of the organ—that is unknown. All they show, if placed in a different order, is certain stages of the ontogeny and certain stages of the degeneration.[1] The ontogeny is shown in figs. 4, 5, 6, and 7, and the degeneration in figs. 6, 8, 10, 11, 12, and 9. These latter figures are a very heterogeneous assemblage, and only show the state of degeneration in a series of forms, and not the phylogenetic degeneration. Seeing that most of the epiblastic cells of Anura contain pigment, I do not see any advantage in placing figs. 2 and 3 in the series at all, while if fig. I has any place in the plate it ought to be last of all.

The phylogeny of the parietal eye is a very difficult problem, and in spite of my former remarks (No. 3, p. 248) I do not think the question can be yet fully solved. Spencer (No. 14, p. 230) has compared its development with that of the paired eyes, which he believes originated as secondary differentiations from the brain—as secondary evaginations. This mode of regarding the problem is easily disposed of, for if the paired and unpaired eyes originated in that way, then in both cases the lens must be the same; and indeed, on physical principles, it is easy to understand that in the paired eyes the lens must of necessity be formed as it is from the lateral epiblast. The anterior wall of

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[1] It is simply a fallacy to suppose that an organ in its degeneration passes through the stages, or even some of them, of its phylogeny.

the optic vesicle, as it grows towards the surface of the body, must catch the light, and this surface is obliged to remain as retina. If the phylogeny of the unpaired eye were the same as that of the paired eyes, the retina would be of the so-called Vertebrate type.

Bütschli (No. 5, p. 178), in dealing with the problems presented by the eye of Pecten, sees the solution in the nature of the lens. It seems to me that here, as in the Vertebrate eye, it is the form of the retina—a closed cup—which gives rise to the cellular lens and the inverted retina.

The appearances that one meets in Pecten are carried still further in the eye of Onchidium. I have, through Professor Howes' and Dr. Günther's kindness, been able to study this peculiar eye, though, as there were not many eyes on the two specimens at my disposal, I could not follow the development. In spite of Patten's off-hand criticism in his paper on "Eyes of Molluscs and Arthropods," Semper was right in his statements that the eye is pierced by the optic nerve, and that thus an eye of the so-called Vertebrate type is formed.

An interesting point in my specimens is that the nerve is double, and enters the optic cup at two points. This, I think, throws light on the way in which the Onichidium eye has developed from an eye of the Pecten type. The nerve-fibres must originally, as in Pecten, have gone round the front wall of the cup to their destination, and their piercing the hinder wall is only a shorter way of getting to their destination.

After all, I think the development does show that the parietal eye is a slightly later development than the paired eyes, but I still hold to the view that the organ has developed in connection with the paired eyes. For this conclusion the two sorts of end elements, rods, and cones, described by me in Petromyzon, are of importance, as is also the fact that fibres have been traced from the thalami optici to the epiphysis.

Most of us now accept the view of Balfour, Carrière (No. 6), and others, that the eyes were once structures opening dorsally on the surface of the unclosed neural plate, somewhat in the fashion of figs. 3 and 16, Pl. XI, of Heape's memoir of the Mole (No. 10).

The parietal eye did not then exist (Pl. VI, fig. A). On the closure of the neural plate the eyes of course got shut in, and in order that no lens of the so-called Vertebrate type should be formed from the epiblast of the median neural line above the eyes, one must suppose that the median suture of the brain was not composed of nervous sensory epithelium like that of the retina (Pl. VI, fig. B). A retinal epithelium of the median dorsal line could not degenerate to form a lens like that of Hatteria. It would be excited by the light, and a lens, if formed, would arise from the indifferent epiblast. A piece of ordinary nervous tissue, on the other hand, would degenerate into an epithelial structure. We have instances of that in the pallium of Teleostei and Ganoids; and such a piece of tissue must be postulated in the median suture of the brain above the paired eyes.

If this be granted, the development of the parietal eye as an apparently unpaired organ is easily explicable. After the closure, according to Balfour, Wiedersheim and others, in their phylogenetic development the paired eyes would receive light from two sources, through the skin of the lateral surface of the body, and through the suture of closure. As they grow towards the surface a portion of the retina of each of them still receives light through the suture, and it is this portion which forms the retina of the parietal eye.[1] Its lens is formed by the epithelium of the suture which we assume is not sensory.

The process of this hypothetical development I have figured in the three diagrams in Pl. VI. The way in which this subsidiary eye could be thus developed from part of the sensory epithelium of the paired eyes is strikingly exemplified in the actual facts of the development of Jacobson's organ in Reptiles from a portion of the olfactory epithelium. Of this development of Jacobson's organ I am preparing a memoir which will soon follow these lines.

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[1] Thus, if no trace of the parietal eye now existed one could arrive at the conclusion that such must once have been the case by induction.

And another instance is shown in the ontogenetic and phylogenetic development of all the complicated parts of the auditory organ from one bit of sensory epithelium. This development of subsidiary sense organs from one piece of parent sensory epithelium is a most remarkable fact of embryology to which I hope to draw the attention it deserves.

Distribution of the Parietal Eye.

These researches show that the parietal eye was developed in the group of Fishes, and still has the characteristics of an eye in the very primitive group of Cyclostomata. It is not impossible that in other fishes it may still present a good development, though it is not very likely that such will be found to be the case in any existing Elasmobranchii and Ganoids.

In this connection a figure in Zittel's 'Palæontologie'[1] seems to me very interesting. It represents the bony skeleton of a Placoderm Ganoid, Asterolepis ornatus, from the Old Red Sandstone, and on the dorsal surface in the centre of a bone, marked os dubium, there is something which looks suspiciously like a parietal foramen.

Why the eye has degenerated can hardly yet be determined. No doubt it has suffered in its competition with the paired eyes. Apparently, too, it was worse fitted out with accessory structures such as muscles, &c., than these.

I shall not attempt to discuss the question of whether it is still functional or not in Cyclostomata. As no lens is developed there it can be of little use as an organ of vision, while I think Wiedersheim (No. 17, p. 149) has made out a good case for its functional use in such forms as Hatteria. In Cyclostomata it has all the characteristics of a degenerate organ, one especially in a very high degree, viz. its variability

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[1] Zittel, 'Handbuch der Palæontologie.' Abtheilung I. "Palæozoologie," Bd. iii, Heft. 1, fig. 161, p. 155.

in different individuals. I have only seen black pigment on it in three Ammocœtes, while the majority of the adult Petromyzon I examined had such pigment in a greater or less degree. I am hence forced to abandon as unlikely the idea that black pigment is formed in the larva, that it then gives place to white, and again in the adult a reversion to black occurs. This seems to me now unlikely, and the only conclusion I can draw is that the pigment is very variable, but that as a rule sooner or later black pigment is formed in the parietal eye of the Cyclostomata.

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DESCRIPTION OF PLATES VI & VII,

Illustrating Dr. Beard's Memoir on "The Parietal Eye of the Cyclostome Fishes."

Alphabetical List of Reference Letters.

ant. Anterior. *bl.* Blood. *br.* Brain. *cn.* Cones of retina. *co.* Coagulated fluid. *c. t.* Connective tissue. *ep.* Epidermis. *gl. trb.* Ganglion trabeculæ. *t.* Lens cells. *md. br.* Mid-brain. n^1. Inner nuclear layer. n^2. Outer nuclear layer. n^2. *gl.* Ganglion of outer layer. *P. E.* Parietal eye. *p. s.* and *p.* Black pigment. *r.* Retina. *rd.* Rod elements of retina. *s.f.* Skull fossa for parietal eye. *sk.* Skull. *s.* Stalk. *th.* Thalamencephalon.

All the figures in Plates VI and VII are from camera lucida drawings, except A, B, and C.

PLATE VI.

Fig. 1.—Longitudinal section through skull of adult Petromyzon planeri, showing parietal eye (*P. E.*) in situ. Zeiss C, oc. 2.

Fig. 2.—Transverse section of ordinary eye of Ammocœtes, drawn under the same magnification as the following figure.

Fig. 3.—Transverse section of parietal eye, taken from the same animal as preceding figure for comparison with it. Figs. 2 and 3 under same magnification, viz. Z. D, oc. 2. These two figures are from one of Herr Schwarz's preparations.

Fig. 4.—Parietal eye of adult Petromyzon planeri in longitudinal section. The only traces of black pigment are present at *ps.* Zeiss F, oc. 2.

Fig. 5.—Parietal eye of Ammocœtes in transverse section. From the second of Herr Schwarz's preparations. Zeiss D, oc. 2.

Fig. 6.—Portion of the retina (*r.*) and lens (*l.*) of the parietal eye of the preceding preparation under high power. Zeiss F, oc. 2.

Figs. A, B, C. Diagrams showing three hypothetical stages in the development of the parietal eye.

PLATE VII.

Fig. 7.—Retinal elements of parietal of an adult Petromyzon planeri under high power. There was no black pigment in the specimen. Zeiss F, oc. 2.

Fig. 8.—Parietal eye of adult Petromyzon planeri, showing position of parietal eye, the skull fossa (*s.f.*), and the distribution of the pigment in the skin over the eye. Longitudinal vertical section. Zeiss A, oc. 2.

Fig. 9.—Parietal eye of an adult Petromyzon planeri, in which there was no pigment on the retina, showing the absence of pigment and of the skull fossa of the preceding figure. Longitudinal vertical section. Zeiss C, oc. 2.

Fig. 10.—Retina of the parietal eye of Herr Schwarz's third preparation. Transverse section. Zeiss D, oc. 2.

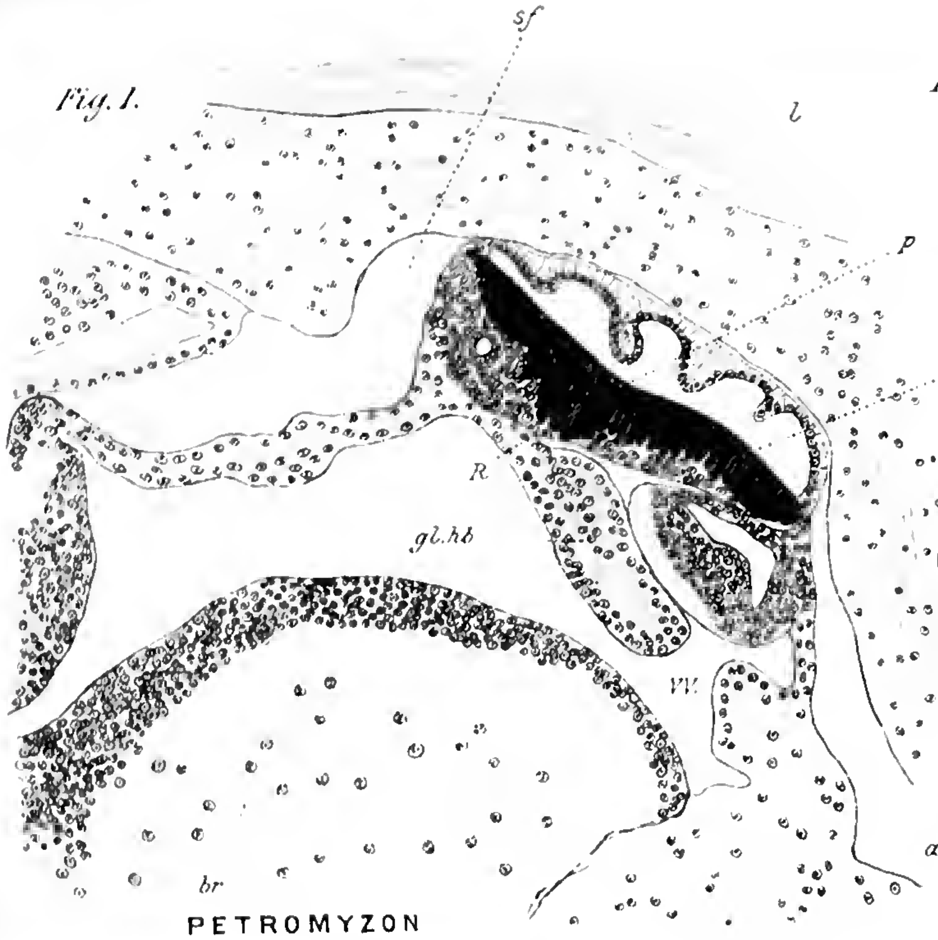
Fig. 11.—Retinal elements of the parietal eye of Myxine glutinosa under higher power. Zeiss F, oc. 2.

Fig. 12.—Longitudinal vertical section of brain and parietal eye of Myxine glutinosa. No pigment in the retina. Zeiss A, oc. 2.

Fig. 13.—Longitudinal vertical section through the parietal eye of an advanced embryo of Anguis fragilis under high power, showing distinct boundary at *B* between lens and retina. Zeiss F, oc. 2.

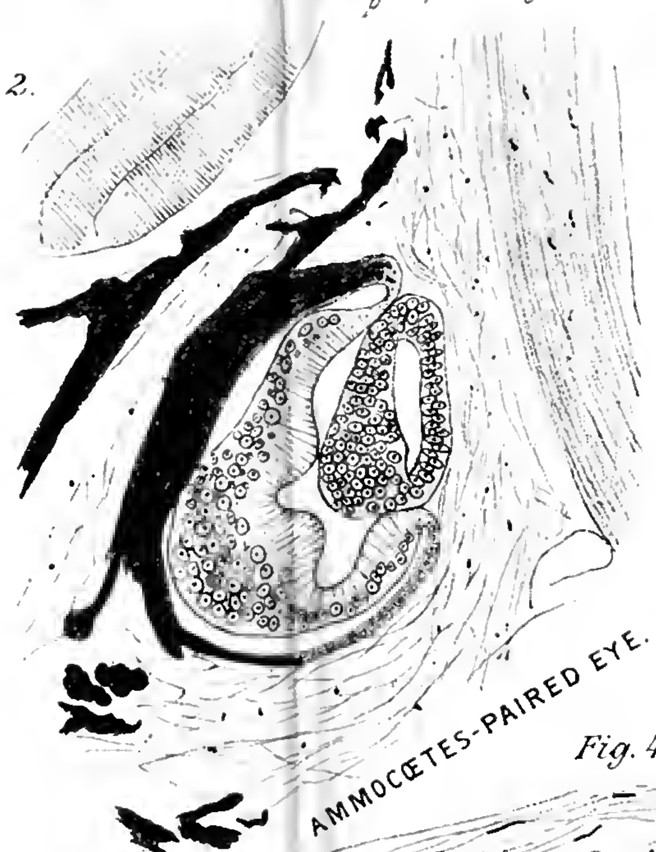
Micr. Journ. Vol. XXIX. N.S. Pl. VI.

Fig. 1.



PETROMYZON

Fig. 2.

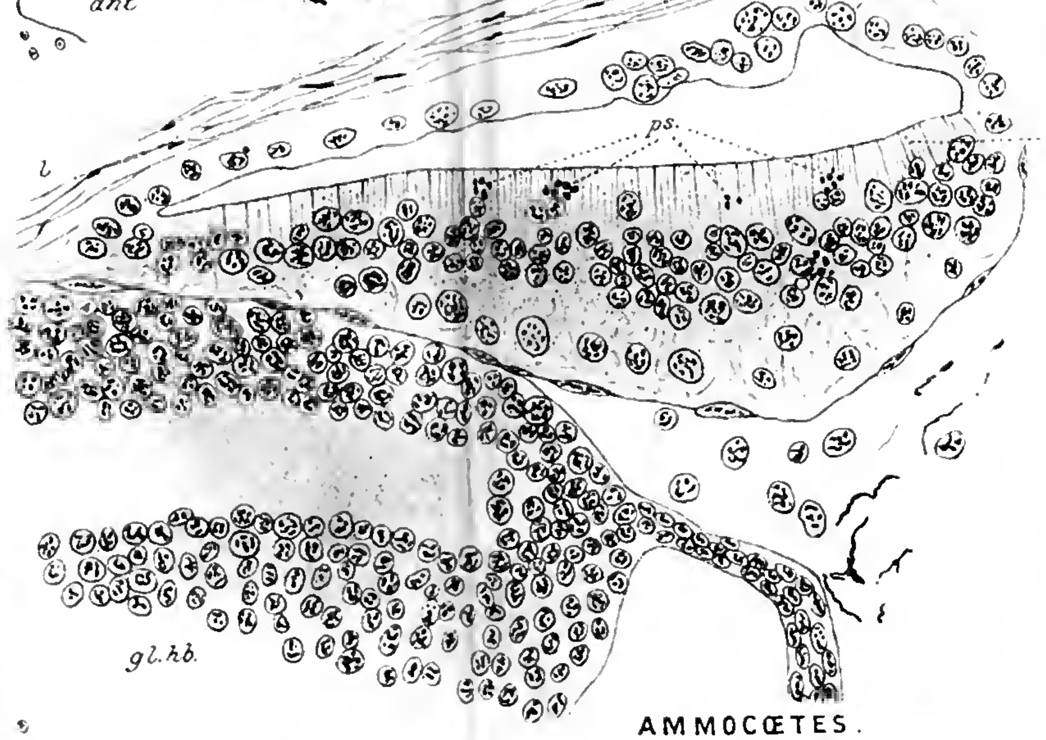


AMMOCŒTES-PAIRED EYE.

Fig. 3.

AMMOCŒTES.

Fig. 4.



AMMOCŒTES.

Fig. 5.

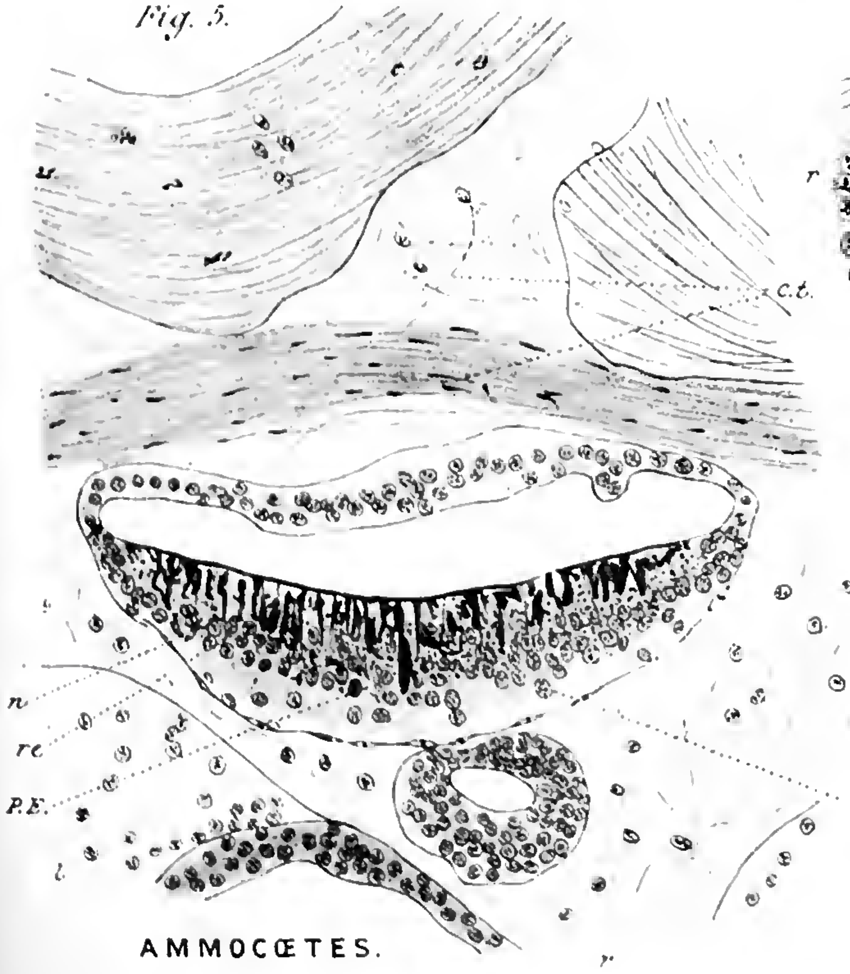


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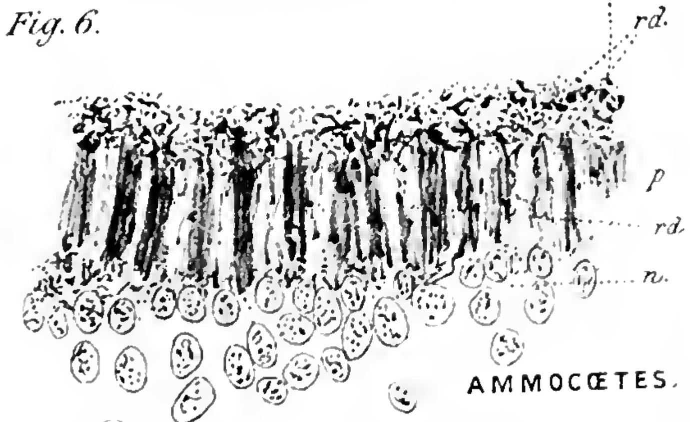
Fig. 6.



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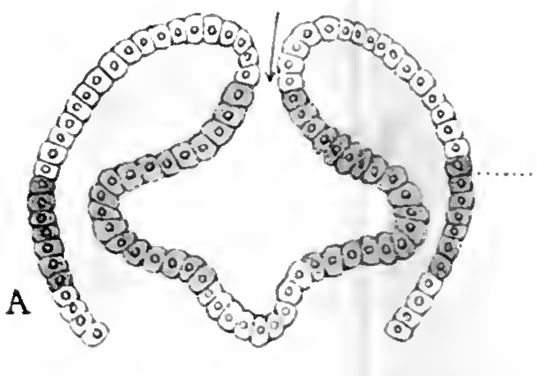

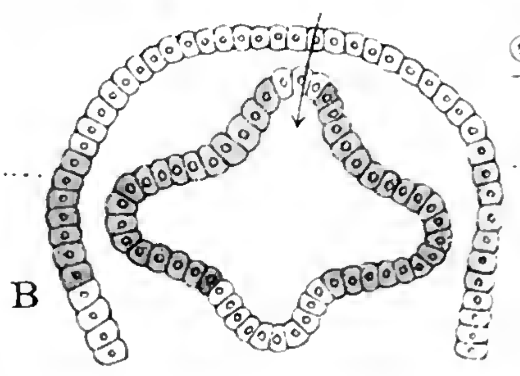

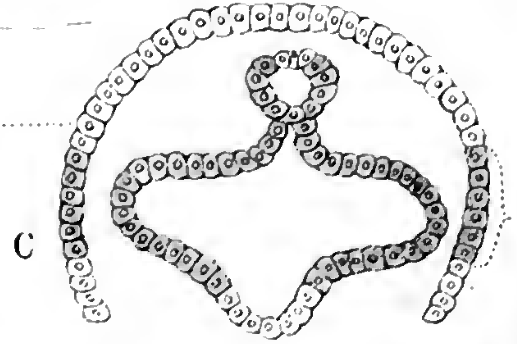

J. Beard del.

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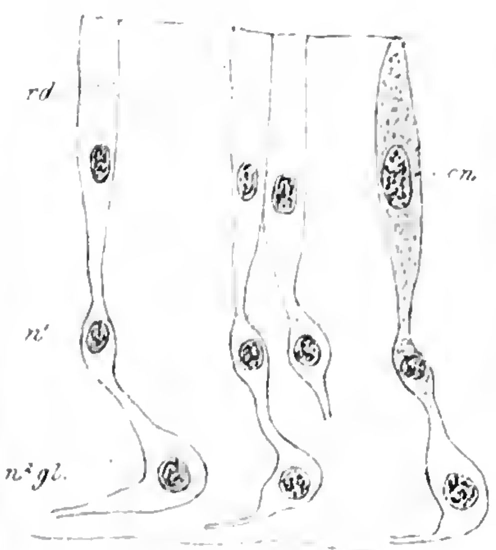
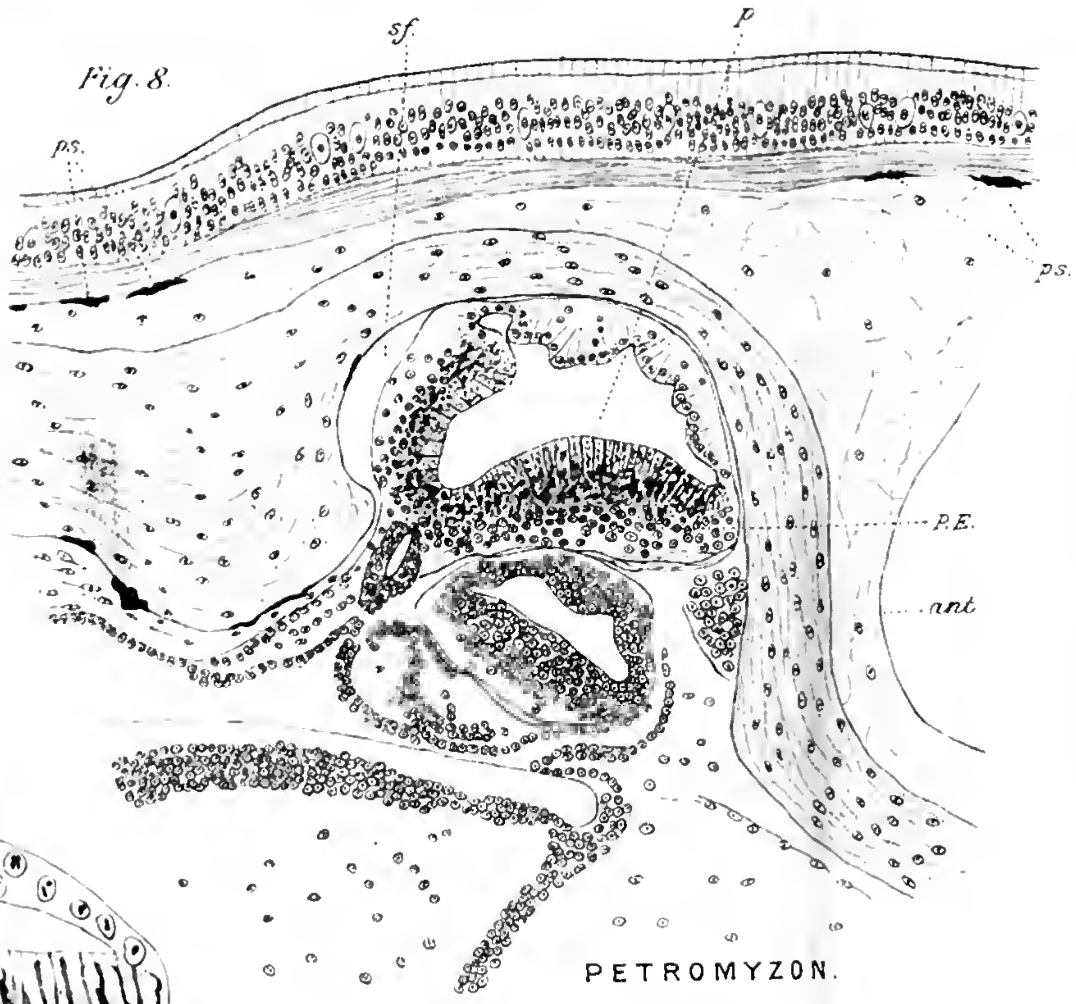
Fig. 7.



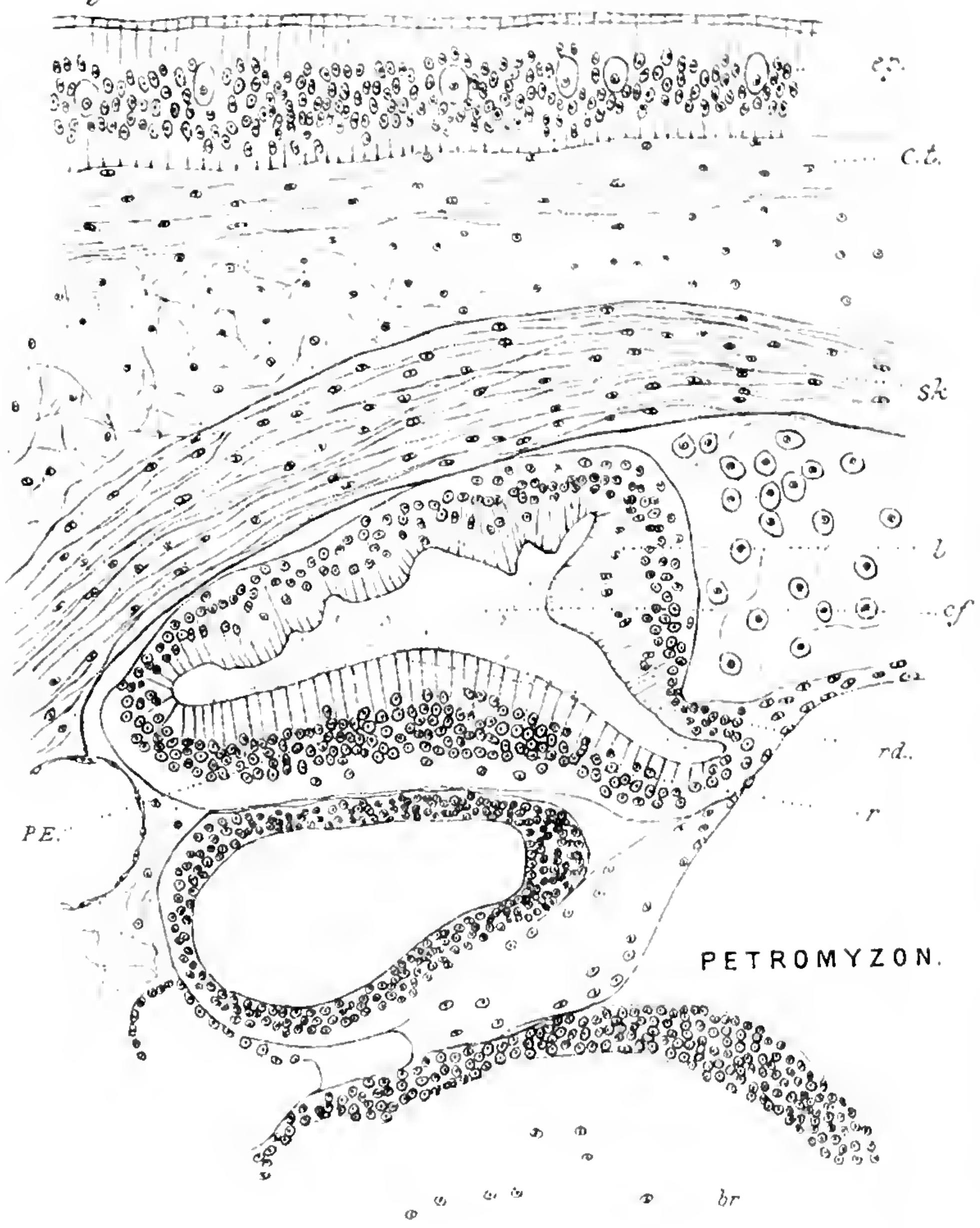
PETROMYZON.

Fig. 8.



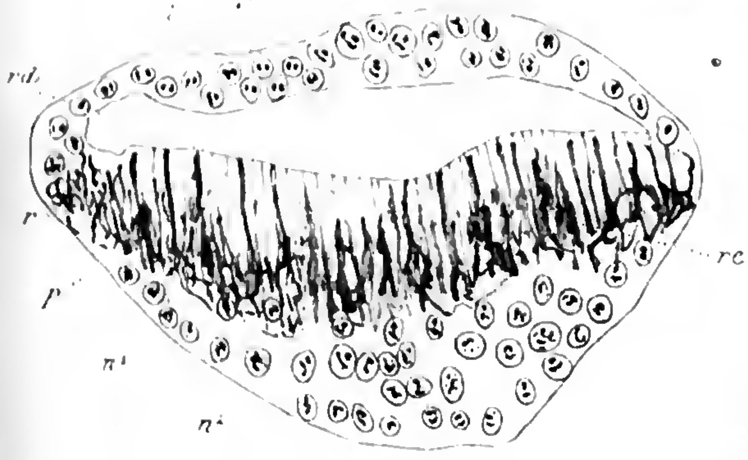
PETROMYZON.

Fig. 9.



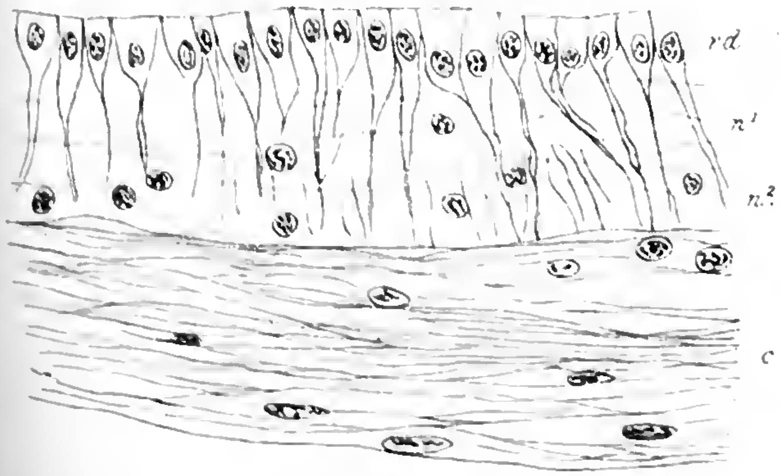
PETROMYZON.

Fig. 10.



AMMOCŒTES.

Fig. 11.

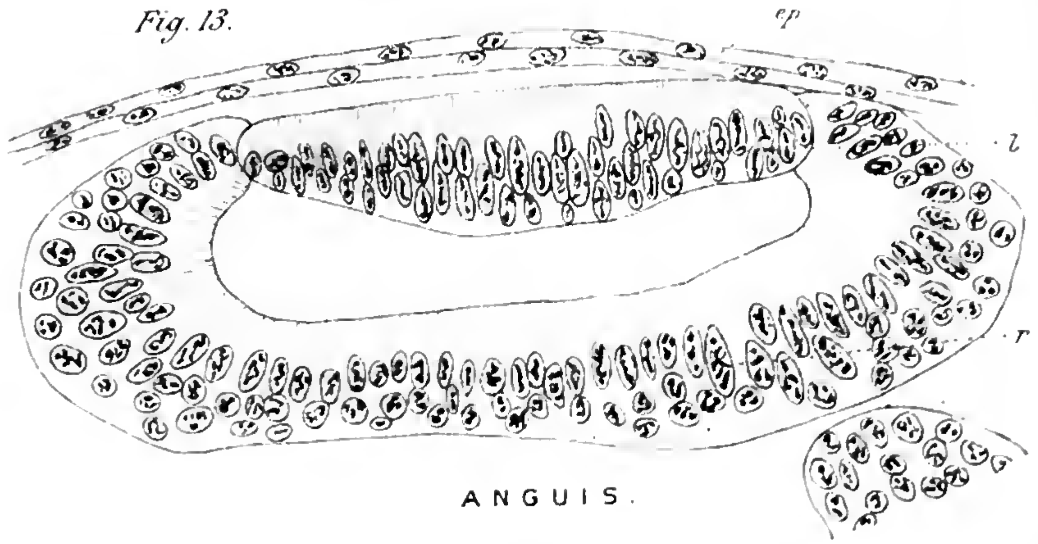


MYXINE.

Fig. 12.

MYXINE.

Fig. 13.



ANGUIS.

J. Beard del.

F. Huth Lith^r Edin^r

On Some Oigopsid Cuttle Fishes.

By

F. Ernest Weiss, F.L.S.,
From the Zoological Laboratory, University College, London.

With Plates VIII, IX, and X,

At the instance of Professor Lankester I have undertaken a careful examination of some of the Cephalopoda forming part of the valuable collection he has gradually acquired for the Museum of Comparative Anatomy at University College, London.

All the species dealt with in this paper belong to the group of the Oigopsida, of whose anatomy and general structure our knowledge is at present still very scanty. This may be said to be especially the case with regard to some of the rarer forms, such as Chiroteuthis and Doratopsis, which I have been enabled to study. Besides these two my paper deals with some points in the anatomy of Histioteuthis Rüppelli, Tracheloteuthis Behnii (Strp.), and Verania sicula (Krohn).

Chiroteuthis, Histioteuthis, and Loligopsis (including the form now called Doratopsis) were all united originally by D'Orbigny[1] (1) in the family of the Loligopsidæ, one of the most important and distinguishing characters of which was the absence of a valve in the siphon.

Brock, in 1880,[2] divided the Oigopsidæ into two groups, the Ommastrephes group and the Loligopsis group. To both he attributed the general Oigopsid characters, which included,

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[1] D'Orbigny, 'Cephalopodes acetabulifères,' 1835.

[2] Brock, 'Morphologisches Jahrbuch,' 1880.

according to him, the slit-like renal openings, loss of accessory nidimental glands, and a uniting commissure between the stellate ganglia. The Loligopsis group he characterised further by the absence of a siphonal valve and the loss of one of the oviducts (the right one in Chiroteuthis Veranyi). This group included Chiroteuthis, Loligopsis, Owenia, and possibly Histioteuthis and Verania, as also devoid of a valve in the funnel.

But the name Loligopsis has now been restricted to the genus formed by Lamarck from a specimen described by Peron and Lesueur, which resembles Sepiola, with the exception of having a rhomboidal fin and only eight arms; and we can therefore no longer adopt the name of Loligopsidæ for a family containing Histioteuthis and Chiroteuthis. Hoyle,[1] in 1886, in his 'Report on the Cephalopoda,' adopts a classification which places Chiroteuthis, Histioteuthis, and Doratopsis, together with other genera (Histiopsis, Brachioteuthis, and Calliteuthis), in a family of Taonoteuthidæ (Steenstrup, 1861), with the single subfamily of Chiroteuthidæ (Gray, 1849). Speaking of the general characters of the family, he says, "There seems to be some uncertainty as regards the presence of a valve; for though the older observers affirm its absence, Verrill, in a species of this genus (Chiroteuthis) of the Northern Atlantic, distinctly affirms that a valve is present; and Professor Lankester informs me that in a Chiroteuthis Veranyi, in University College Museum, London, there is a very small, in fact a rudimentary, valve, just a transverse fold, not projecting much, and that he has acquired a Histioteuthis with a well-developed valve in its funnel."

I am able to confirm these observations of Professor Lankester, and to add several new points to what little was known before of these very interesting forms. The careful examination of these forms leads me to uphold the uniting of Chiroteuthis, Doratopsis, and Histioteuthis into one family, as is done by Hoyle, and was done also by D'Orbigny, though the classification of the latter was based on many erroneous observations; but

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[1] W. E. Hoyle, 'Report of H. M. S. Challenger,' "Zoology," 16, 1886.

the new facts I have been able to make out will place the Chiroteuthidæ in a different relation to the remaining families of the Oigopsida, and will necessitate a slight change in the classification of this group, which I shall suggest at the close of this paper.

I shall begin with the consideration of the type genus of the Chiroteuthidæ, the species being the one named after Vérany, and figured both by D'Orbigny (1) and by Vérany.[1]

CHIROTEUTHIS VERANYI (Férussac), D'Orbigny.

The specimen I examined was slightly smaller than the one of which Vérany gives measurements in his description. It was purchased at Nice by Professor Lankester for the Museum of University College. The lengths of this specimen are as follows:

Body without arms, but including fin	11·2 cm.	
Fin (length)	3· ,,	
,, (breadth)	3·5 ,,	
Breadth of body	2· ,,	
1st arm	9· ,,	
2nd ,, ...	11·2 ,,	
3rd ,, ...	12· ,,	with a median fin.
4th ,, ...	17·3 ,,	with lateral external fin.
Tentacular arms	8· ,,	

The order of the arms in descending order of the lengths is 4, 3, 2, 1, which order is also given by Vérany, though, owing probably to a printer's error, the measurement for the third arm is given as the smallest. Each pair of arms is provided with two rows of suckers, which are well figured by D'Orbigny, the fourth pair of arms being, besides, provided with a row of deeply-pigmented warts, somewhat like those which occur all over the body of Histioteuthis, and are possibly phosphorescent organs.

The tentacular arms are exceedingly long, and carry modified suckers at varying intervals along their whole length. The club has modified suckers, as figured by D'Orbigny, and is provided with two lateral-fluted webs (Shutzmembranen).

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[1] Vérany, 'Cephalopodes de la Mediterranée,' 1851.

The buccal membrane is large, drawn out into seven points, and is devoid of suckers.

The nuchal cartilage is flattened, and of what von Ihering[1] (5) calls the Sepia type.

The fastening of the mantle to the base of the siphon (Pl. VIII, fig. 4) is by two depressions on the funnel, complicated by a lateral tooth, and by triangular cartilages on the mantle.

The interior of the funnel is provided with a valve (Pl. VIII, fig. 5) near its apex, which is drawn somewhat to a point in the centre. It is small, but not rudimentary, though it seemed smaller on first observation, as it adhered to the dorsal wall of the funnel.

Midway between the eyes and the funnel on the ventral (infundibular) side of the body are two spoon-shaped organs, like those figured for Chiroteuthis lacertosa by Verrill[2] (6), but which have neither been described nor figured for Chiroteuthis Veranyi by D'Orbigny nor by Brock. They possess a small ganglion at their enlarged base, which seems to be supplied by a nerve from the cerebral ganglia, and I regard them as at all events originally olfactory in function. I will, later on, point out their homology to the olfactory organ of other Cephalopoda, and with regard to the other groups of Mollusca, Professor Lankester has suggested to me that they might be homologous to the Gasteropod tentacle.

The body of Chiroteuthis is elongate and very small compared to the size of the head and arms.

On opening the mantle cavity we find the rectum with anal appendages not reaching up to the base of the siphon.

The ink-sac is short, triangular in shape, and bears on its surface two glandular organs, which in position especially greatly resemble the accessory nidimental glands in Loligo, which resemblance is increased by the relation to these organs of the branches of the visceral nerves (Pl. VIII, fig. 5). These organs are visible in Vérany's figures by transparency (Pl. 39).

Ventrally and slightly anterior to the base of the gills are

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[1] von Ihering, 'Zeitschrift für wissenschaftliche Zool.,' 1881.

[2] Verrill, 'Transactions Connecticut Academy,' 1882.

two well-developed renal papillæ (Pl. VIII, fig. 4), which papillæ are continued and expand beneath the wall of the renal chamber (Pl. VIII, fig. 5).

At the side of the gills, coming up behind them, are the oviducts without terminal oviducal glands. These glands are halfway up the duct (Pl. VIII, figs. 6 and 7), and below the glands the oviduct shows an annular marking and narrows down to a small opening into the cœlom (Pl. VIII, fig. 7). As I mentioned before, Brock (2) asserts that the right oviduct is absent in Chiroteuthis Veranyi, which I find, in this specimen at least, is not the case. Chiroteuthis does not, therefore, differ from the general Oigopsid type in this character.

Far back in the body are two nidimental glands (Pl. VIII, fig. 4), the existence of which is denied by Brock (2). They are narrow and long, but show distinctly the structure of a nidimental gland (Pl. VIII, fig. 8).

On opening the renal chamber we find it to be a single one, like that figured by Vigelius[1] (7) for Ommastrephes, and which Grobben[2] (8) takes to be typical for Oigopsida. There is no true dorsal renal chamber, but a more anteriorly situated division of the single chamber (fig. 7).

The vena cava passes down the right side of the ink-sac, and divides close to its entrance into the renal chamber into two renal veins, which receive two branches from the mantle.

Two distinct viscero-pericardial apertures lead from the renal chamber to the cœlom (Pl. VIII, figs. 5, 6 and 7). The pericardial portion of the cœlom contains the heart, which is large and broad, especially in the ventricular part. The posterior portion of the cœlom contains the stomach, which reaches far back, the cæcum and the ovary.

The branchial hearts lie in diverticula of the cœlom. The ovary partly overlies the stomach and is attached at two points anteriorly to the stomach and posteriorly to the wall of the cœlom, as Brock has laid down for all Oigopsida[3] (9) (fig. 7).

[1] W. T. Vigelius, 'Niederlandisches Archiv für Zoologie,' 1880.

[2] C. Grobben, 'Arbeiten des zool. Instituts zu Wien,' 1884.

[3] Brock, 'Zeitschrift für wissenschaftliche Zoologie,' 1882.

I was not able to make out any commissure connecting the stellate ganglia, which was, perhaps, owing to my not being able to dissect to the uttermost this valuable specimen which was to be remounted for the Museum.

The pallial nerve is given off from the stellate ganglion itself.

DORATOPSIS VERMICULARIS (Rüppell), DE ROCHEBRUNE, [LOLIGOPSIS VERMICULARIS (Vérany)].

Plate IX.

The specimen studied by me was obtained at Messina, and was presented to Professor Lankester two years ago by Professor Kleinenberg, of the University of Messina, together with several rare Cephalopoda.

From the excellent drawings of this specimen made by Miss Stone, several interesting points can be made out which are not given by Vérany in his Pl. 28, *a*, *b*.

The general proportions of the specimen I examined, which was considerably smaller than the one described by Vérany, differ considerably from those of the latter.

Compared with Miss Stone's drawings, which are very accurate, Vérany figures the fourth pair of arms too short and stout, and the three other pairs too long. The region between the base of the arms and the eyes is too long, the neck too thin, and the spine at the end of the body too long in fig. *a*. In fig. *b* the spine is too broad, its length being about right.

In neither figures does he show what I shall presently describe as the stellate organs and the olfactory organs respectively.

The order of the arms is as in Chiroteuthis, 4, 3, 2, 1, and the tentacles exceed the fourth pair in length. The arms, 1, 2, and 3 are very short compared to the size of the body, with no dorsal webs or fins, and bear two rows of small sessile suckers.

The fourth pair of arms are enormously large compared to the others, more transparent and thicker than the tentacular arms. They possess only one row of suckers disposed at greater intervals.

Pfeffer[1] (10), however, says that they seem to have a double row of suckers, but here he is mistaken.

The fourth arm, indeed, has a broad lateral expansion similar to that of Chiroteuthis, and this expansion bears small thickenings which correspond to the ridge-like projections on the lateral membrane of the club of Chiroteuthis.

Verrill, in Leptoteuthis diaphana, which is really a Doratopsis, figures two rows of suckers and pigment spots, like those of Chiroteuthis, on this fourth pair of arms.

The tentacular arms are long and terminate gradually in club-like expansions, bearing circular sessile suckers in four rows. These extend some way down the arm. The club is provided laterally with a protecting membrane (fig. 7).

The mouth is surrounded by a thick papillate lip and a narrow buccal membrane (Pl. IX, fig. 4).

The eyes are large, but not pedunculate, and their opening has no lachrymal sinus.

Somewhat below the eyes, on the ventral side of the body, project two small organs (fig. 3, *olf. org.*), which seem to be supplied by nerves, and must, I think, be taken as homologous with the spoon-shaped organs of Chiroteuthis, and olfactory in function.

On the dorsal side of the cerebral nervous mass two reddish spots are noticeable, the nature of which I was not able to ascertain.

Behind the cephalic mass we find a very much elongated and almost perfectly transparent neck region. This portion of the body presents an appearance like that of segmentation, by a series (8 in this specimen) of plates with radiating margin lying along the median dorsal line. These organs, shown enlarged in fig. 6, overlie directly the two strangs of visceral nerves, and seem supplied by branches from the aorta. I shall call them the stellate organs.

The alimentary canal passes along the side of the aorta, the vena cava along the ventral side of the neck.

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[1] Pfeffer, 'Abhandlungen des Naturwissenschaftlichen Vereins,' Hamburg, 1884.

The mantle is attached to the head or rather neck by a cervical plate of cartilage, somewhat narrower in proportion than that of Chiroteuthis.

The mantle fastening by tooth and socket on the siphon is almost identical with that of Chiroteuthis (fig. 5).

The apical portion of the funnel is bent almost at right angles to the body, and when opened a valve is seen just below the bend. The valve is proportionately stronger than in Chiroteuthis. On the ventral side of the funnel are two glandular pads, which I can only compare with those found in Verrill's organ (fig. 3).

On opening the mantle two very short papillæ may be seen leading into the renal chamber, which is short and broad notwithstanding the elongation of the body (fig. 5).

The specimen examined was sexually not well differentiated and probably still young. There were no nidimental glands present, and there seemed to be only one genital duct on the left side. I took it to be a male specimen. The female, I think, would have shown two oviducts and nidimental glands considering its general concordance with Chiroteuthis.

The pallial nerve came direct from the stellate ganglion.

Dimensions of Body.

Entire length of body without arms . .	5·2	cm.
Length of fin	1·1	„
Breadth „	1·	„
Spine beyond fin	·8	„
Edge of mantle to beginning of fin . .	1·8	„
„ „ to eyes	1·2	„
Arm 1	·12	„
„ 2	·23	„
„ 3	·28	„
„ 4	1·5	„
Tentacular arm	2·4	„

The spine at the end of body bears several swellings which seem to be of a glandular nature.

Histioteuthis Rüppelli (Vérany). Pl. X, figs. 8—12.

The specimen examined by me was purchased at Nice in 1886, by Professor Lankester, for the museum of University College.

The general external features are noted by Vérany. The suckers of the short arms are pedunculate, globular, and show four large teeth on the upper margin of the chitinous ring. The suckers of the tentacular clubs are sessile, and have teeth all round the chitinous ring.

The tentacular club is badly represented by Vérany, and resembles more that figured for Calliteuthis by Hoyle (3). Its extremity is drawn out into a narrow strip with suckers in two or three rows. As the club expands we get four rows, two of which have much larger suckers than the other two. The club has a median dorsal fin, extending along the distal half, and an external lateral fin along the proximal half of the club. On the internal margin of the club are some small suckers and cushions or pads, alternating, and forming the fixing apparatus of the tentacles. These suckers and pads, thirteen to fourteen in number, extend, with gradually enlarging intervals, about halfway along the arm (Pl. X, fig. 12).

The eyes are large, but show no lacrymal sinus. Between the eye and funnel, and situated ventro-laterally, are two lappets supported by a strong nerve, lappets which are homologous with the spoon-shaped organs of Chiroteuthis, and the similar projections in Doratopsis (Pl. X, fig. 5).

The neck shows slight transverse and short longitudinal ridges, corresponding in position, but very slightly in development, to those of Thysanoteuthis (*tc.* and *lc.* figs. 5 and 7, Pl. X).

The small longitudinal ridges have been called olfactory crests by Verrill (6) in Ommastrephes, where they are prominent, and divide the neck region into separate areas or facets; but only in the most ventral of these, i.e. the one nearest the siphon, is found, in Thysanoteuthis, a small separate crest, which is the homologue of the olfactory lappets of

Histioteuthis. In connection with this ridge, probably along its base, as being there protected, will be found the sensitive epithelium. In Ommastrephes the ridge in the ventral facet is very small, and seems to be partly introverted into the skin. Here I found a sensitive, or at least a highly modified, epithelium, which I will describe later on.

The nuchal cartilage is more elevated and narrower than in Chiroteuthis, and more of the Ommastrephes type.

The depressions at the base of the siphon are elongate, broader aborally, and tending to separate into two fossæ. The cartilage on the mantle wall is elongate, pear-shaped, and less definite and prominent aborally (Pl. X, fig. 11).

The siphon is provided with a strong muscular valve, as has been already stated by Professor Lankester (Pl. X, fig. 10).

The gills are very powerfully developed. Two strong muscular renal papillæ are situated somewhat anteriorly to the base of the gills and on either side of the rectum (Pl. X, fig. 11).

Two large nidimental glands, on the same level as the base of gills, but median to them, project freely into the mantle cavity (Pl. X, fig. 11).

Two oviducts, with terminal glands, open dorsad of the gills between their base and the renal papillæ. At the end of the oviducal gland proper (*gl.*) there is a further glandular structure, corresponding minutely in structure with the nidimental gland, but about twice the size, and, indeed, almost as large as the remainder of the oviduct. The external opening of the oviduct extends about halfway along this gland. The oviducts correspond so closely with those of Thysanoteuthis rhombus, figured by Brock,[1] that they might stand as a drawing of those of Histioteuthis. The internal openings are slit-like and situated near the lower end of the cœlomic cavity, thus differing from the oviducts of Chiroteuthis, which are short, and open far up into the cœlom. The beginning of the oviduct shows a glandular passage.

On opening the renal chamber it is found to be comparatively long, containing the vena cava and renal veins, with

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[1] Brock, 'Zeitschrift f. wiss. Zoologie," 1882.

their renal covering, and the hepatic ducts, with renal tissue in bunches at intervals. Two very distinct membranous funnels lead from the renal into the cœlomic cavity. The cœlom is not distinctly divided into two parts. The heart lies far back, and the ovary passes underneath the heart to its anterior attachment on the stomach. Posteriorly the ovary has another point of attachment, here to the cœlomic wall.

The genital artery is given off from the posterior aorta, and passes over the front of the heart. The cœlom communicates freely with the space containing the branchial hearts.

Most points in the anatomy of Histioteuthis lead, as I will point out afterwards, to a close association of this form with Thysanoteuthis.

TRACHELOTEUTHIS BEHNII (Steenstrup).

The specimen examined (one of those captured at Messina, and presented by Professor Kleinenberg to Professor Lankester) agreed very closely with the description given by Pfeffer (10) of Verilliola nympha, and therefore in all probability Hoyle is right in identifying the two genera. It certainly agrees with Steenstrup's[1] (12) account of this species. The order of the arms in descending order of lengths was 2, 3, 4, 1.

The second and third arm are very nearly equal, as may be seen from the actual measurement appended. The suckers of these arms, too, are much larger than those of the other arms. They are provided with slight membranous fins, as is also the fourth pair of arms (Pl. X, fig. 1).

The tentacular arms are relatively long, with a distinct club at the extremity. The suckers near the distal end are large and in four rows, but proximally pass over into the stalk in ight or ten rows of very minute suckers (Pl. X, fig. 3).

The club is provided with a lateral fin-like expansion, as in Doratopsis.

The eyes are large, but not very prominent.

On the back of the head are two pairs of large pigmented

[1] Steenstrup, 'Vid. Meddel nat. Foren Kjobenhavn,' 1881.

patches, such as Pfeffer describes. On the ventral side of the head, close beneath the eyes, are two small organs, probably with sensory function. These organs agree most closely with those of Sepiola, which lie exactly in the same position, and are represented by a small elliptical ring, which probably protects the sensitive epithelium at its centre. An olfactory crest, homologous with that of Sepia, is absent in Sepiola and Tracheloteuthis. A fine nerve seems to pass over the ocular region to this sense organ (Pl. X, fig. 2, *n.*).

The neck of Tracheloteuthis is very long and thin, and the mantle edge seems therefore loose and wide. The cartilaginous fastening of the mantle at the base of the funnel is simple, and like what we find in Architeuthis and in Loligo.

The interior of the funnel seems at first devoid of valve, though, according to Steenstrup (12), it possesses one (i. e. in Tracheloteuthis Riseii). But the funnel has what Verrill has described in Desmoteuthis, and what Hoyle has called Verrill's organ. At the upper part of this organ, however, a distinct though small valve is present, partly overlapped by the median portion of Verrill's organ (Pl. X, fig. 4).

Whatever may be, therefore, the exact nature and function of Verrill's organ, whether mucoid or sensitive, though mechanically it aids in closing the funnel, it does not preclude the presence of a valve.

Besides the median portion of Verrill's organ, which seems composed of several parts, there are two lateral cushions on the anterior wall of the siphon (fig. 4, *lp.*).

These lateral pads, though not so strongly developed, are seen in Doratopsis (Pl. IX, fig. 8), and in Histioteuthis (Pl. X, fig. 10). Both lateral and median portions of Verrill's organ are absent in Chiroteuthis.

On opening the mantle cavity we notice the characteristic position of the viscera at the extremity of the body, and the consequent development of the depressores infundibuli muscles, in the middle of which runs the vena cava. The gills, too, have been drawn out from back to front, and are thin and loosely branched. The viscera in general aspect resemble those of Doratopsis. The apertures I was unable to make out on account of the smallness of the specimen. The same is the case with regard to the sex of this specimen.

Its measurements were:

Length of body	2·7 cm.
,, mantle	2·1 ,,
,, fin	·6 ,,
Breadth of fin	·8 ,,
Arm 1	·32 ,,
,, 2	·75 ,,
,, 3	·6 ,,
,, 4	·4 ,,
Tentacles	1·35 ,,

Tracheloteuthis, though in many points agreeing with Doratopsis, is, I think, better placed now by Hoyle among the Ommastrephidæ.

VERANIA SICULA (Krohn). Pl. VIII, figs. 1—3.

In its main features this species resembles Enoploteuthis, e. g. shape of fin and suckers modified into hooks, and is classified together with Enoploteuthis. The specimens studied by me were sent from Messina by Professor Kleinenberg to Professor Lankester.

The arms, according to length, are 2, 3, 1, 4. Each arm has at its extremity a small swelling preceded by eight to ten pairs of modified suckers, and according to Pfeffer (10) these are hectocotylized portions, just as we find them on the fourth pair of arms in Enoploteuthis.

The tentacular arms are very short and thin, and the club bears only a few suckers, three of which are relatively very large. These suckers are narrow, but do not bear hooks (fig. 3).

The tentacular arms were not observed by Rüppell or Krohn, and Vérany thought that they were regularly lost at a certain stage.

The specimen I examined was very much smaller than those previously described, and probably still quite young. Brock

(2) thinks that such a form regularly losing its long arms points to the way in which the Octopoda gradually developed from the Decapoda.

The eyes are not pedunculate, nor indeed prominent.

Behind the eyes is a small patch representing the olfactory sense organ, and connected by a nerve with the main cerebral mass (fig. 2, *olf. org.*).

Sections taken through this organ show a cushion of many-layered epithelium cells, some oval and some spindle shaped, and sunk away from the surface, and supplied with nerves from the ganglion, which lies beneath the cushion. They resemble greatly the sensitive cells figured and described by Sochaczewer[1] (13) in the pedal gland of the Snail. The cilia, if present, are very short; probably there are only sensitive hairs, and not cilia proper, which would be unnecessary, as the surface is exposed to the free play of the water. Mucous cells seem absent.

I take this to represent the simplest form of cephalic olfactory organ in Cephalopoda, as in sections of embryos of Loligo and Ommastrephes I have found this patch with similar modified cells situated in about the same position behind the eyes. Indeed, on a surface view of a young Ommastrephes it forms a very conspicuous elongated knob laterally and posteriorly to the eye.

In the nearly related form Enoploteuthis this organ is more prominent than in Verania.

In Onychoteuthis it is represented by a ridge, and when we get strong cervical ridges developed as in Thysanoteuthis, we find it, as mentioned before, as a small lappet in the corner of the partition formed by these ridges (Pl. X, fig. 7).

In Histioteuthis, where these ridges become much reduced, the lappet seems relatively larger but occupies the same position; and this form leads on to Chiroteuthis with its spoon-shaped organs, and Doratopsis with its stalked and club-shaped processes.

Unfortunately sections across the processes in Histioteuthis and Chiroteuthis do not reveal any modified epithelium cells

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[1] Sochaczewer, 'Zeitschrift für wiss. Zoologie,' 1881.

though a strong nerve supply exists in these organs. Possibly they have changed their function and become tactile in nature, in Chiroteuthis at least.

I hope, however, at some future date to be able to give some further account of these organs.

Taking another set of forms we can pass from the olfactory ridges on the embryo of Ommastrephes to its adult stage, where there is still a specialised mass of cells similar to those of Vérania at the base of the ridge, as I was enabled to find in sections of the ridge.

Then in Loligo we get the olfactory organ partly invaginated but keeping the same relation to the ridges on the neck, which become now specialised into an auricular, or better, a protective crest (Pl. X, fig. 6).

Verrill (6) speaking of the auditory pore of Ommastrephes illecebrosa, must surely mean the structure which is generally looked upon in Loligo and Sepia as an olfactory pit, or, at least, as a sense organ, which is of the nature of an olfactory or gustatory organ.

In Sepia sections of this pit show a similar structure to the modified epithelium before mentioned, and the presence of ciliated cells in large numbers indicate that a current must be constantly kept up in the interior of the pit, bringing olfactory particles to the sensory cells.

In Octopus and Eledone the pit is not protected by a crest, but situated in an equally well-protected spot at the junction of the mantle with the neck. In Octopus the pit is lined with epithelium exactly like that of Sepia, so I think this olfactory organ may be traced successively in the different groups of Cephalopoda from the spoon-shaped organs of Chiroteuthis to the invagination of Sepia and Octopus, both being the extreme developments of the olfactory patches or cushions seen in Verania. The series reminds one of the transition of the olfactory organs of fishes from external processes to pits, described by Professor Wiedersheim last year in his paper before the British Association at Manchester.

The fastening of the mantle in Verania consists of a simple pyriform groove at the base of the funnel with a corresponding ridge on the mantle (fig. 2).

The siphon is provided with a modification of Verrill's organ, but has also a valve relatively near its base and connected with the median portion of Verrill's organ. There are also two large lateral cushions on the anterior wall of the siphon, as noticed in Doratopsis and Tracheloteuthis. Perhaps these structures are relatively large in these forms owing to their being all still very young, and they may perhaps disappear at a later stage, since they have not been described for the larger specimens examined by Vérany, Brock, and others.

The viscera of Verania showed no features worth special notice; I was unable to make out much owing to the smallness of the specimen.

Measurements.

Length of body	1·4 cm.
„ fin	·7 „
Breadth of fin	1·4 „
Length of mantle	·7 „
Arm 1	·7 „
„ 2	1·2 „
„ 3	1· „
„ 4	·6 „
Tentacular arms	·7 „

CONCLUDING REMARKS.

It will be seen from the above investigation of several of the members of the Chiroteuthidæ, that differing though they do on some points and especially in general appearance, we may justly unite them in a single family, though not on the grounds formerly given for their separation from the other Oigopsida, namely, the absence of siphonal valve, loss of accessory nidimental glands and of one of their oviducts.

The concordance of Chiroteuthis with Doratopsis is very complete indeed, as regards, for example, the fastenings of mantle, the relative length of arms and tentacles, the projecting olfactory processes, &c. Their main difference is in the relative form of body and in some points of detail, as, for example, the stellate organs and pigment spots, and the absence of Verrill's organ in Chiroteuthis which is present in Doratopsis.

Some of the main points of agreement between Histioteuthis and Chiroteuthis, besides shape and proportion of body, are the pigmented (phosphorescent?) organs on the body and arms, the suckers (modified) on the tentacular arms, and, perhaps above all, the presence of renal papillæ in both Chiroteuthis, and Histioteuthis, which Vigelius,[1] (14) in describing those of Thysanoteuthis rhombus, believed to occur only in that member of the group of Oigopsida.

Besides this they agree in the course of the vena cava, the single renal chamber, and the extent of the cœlom. On the other hand, now that the great differences which separated the Chiroteuthidæ from the other Oigopsidæ, notably the absence of siphonal valve, single oviduct, &c., have been disproved, I see no reason why we should not place the subfamily of Chiroteuthidæ in the family of Ommastrephini side by side with the subfamilies of Thysanoteuthidæ, Ommastrephidæ, and Mastigoteuthidæ, and thus abolish the family of Taonoteuthidæ, the name of which was not distinctive nor descriptive of any of its genera. The Chiroteuthidæ have some points in common with all the subfamilies of the Ommastrephini, but especially many and indeed important ones with the Thysanoteuthidæ; and I should place the Chiroteuthidæ next to this subfamily on account of the following points of agreement.

The short arms of both Thysanoteuthis and Histioteuthis are not so unequal as are those of Chiroteuthis. In Thysanoteuthis[2] they are protected by two large, fluted, membranous folds, which might easily be developed into the connecting umbrella of Histioteuthis.

The long arms in Histioteuthis and Thysanoteuthis agree strikingly. The club has in both four rows of suckers, two of

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[1] Vigelius, 'Mittheilungen der zool. Station Neapel,' 1881.

[2] Two specimens of Thysanoteuthis rhombus are preserved in the museum of University College, and have been placed at my disposition for study. They were obtained by Professor Lankester from the Zoological Station of Naples.

which are much larger than the other two, and all along the arm we have an almost identical row of alternating suckers and pads or fixing cushions, which Steenstrup[1] (15) gives as a main character of the whole family of Ommastrephini.

In speaking of the olfactory organ I spoke of the agreement of the cervical ridges of Histioteuthis with those of Thysanoteuthis, which are only reduced in prominence in Histioteuthis, and are more strongly developed than in Tracheloteuthis, and other forms which are actually included in the Ommastrephidæ.

The mantle fastening in Histioteuthis is more simple than that figured for Thysanoteuthis by Troschel,[2] (16) from which it only differs by the reduction of the tooth which projects over the longitudinal depression at the base of the funnel.

Another point on which great stress has been laid by Vigelius (14) is the presence of the renal papillæ, usually absent in Oigopsida but occurring in Thysanoteuthis, Histioteuthis, and Chiroteuthis.

Of the striking agreement of the oviducts in Histioteuthis and Thysanoteuthis I have spoken before in treating of Histioteuthis. The same is the case with the large nidimental glands which project and hang freely into the mantle cavity. In both, too, the ovary reaches far forward in the cœlom, and is attached by two points and not along its entire length.

In fact Thysanoteuthis agrees more nearly with Histioteuthis than with Ommastrephes with regard to its anatomy. The stellate ganglia in Histioteuthis are invested by a very strong commissure, which does not exist in Thysanoteuthis according to Vigelius (14), but which brings Histioteuthis in accord with the other Ommastrephini. In Chiroteuthis I was unable to discover such a commissure.

Chiroteuthis has several points of agreement with Ommastrephes, viz. the complicated fastening of the mantle, the position and structure of the oviducts and nidimental glands.

Then Chiroteuthis agrees in many points with Architeuthis,

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[1] Steenstrup, 'Oversigt Kong. Danske Vidk. Skels. Forh.,' 1880.

[2] Troschel, 'Archiv für Naturgeschichte,' 1857.

also a member of the Ommastrephidæ, and the same may be said of Doratopsis, which Pfeffer has classified so closely with Tracheloteuthis (his Verrilliola).

Even Mastigoteuthis has affinity for one of the Chiroteuthidæ, for Verrill (6) mentions an olfactory lappet which I find is like the one I have described for Histioteuthis, though his mention of an auditory pore is puzzling.

Taking all these points into consideration, I think we may safely dispense with the family name of Taonoteuthidæ, and place the Chiroteuthidæ as a subfamily under the Ommastrephini.

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DESCRIPTION OF PLATES VIII, IX, & X,

Illustrating Mr. F. Ernest Weiss's Paper, "On Some Oigopsid Cuttle Fishes."

PLATE VIII.

Figs. 1—3.—Verania sicula.

Fig. 1. Dorsal view of the entire animal. *h.* Hectocotylized end of the arms. *t.* The short tentacular arms. *s. g.* Stellate ganglia.

Fig. 2. Ventral view after opening the mantle cavity, and the funnel along the median line, showing *olf. org.*, the olfactory organ, the valve with the median portion of Verrill's organ and its lateral pads (*l. p.*) and central pads (*c. p.*). *r.* Kidneys. *ov.* Gonad. *br. heart.* Branchial heart.

Fig. 3. *a.* The tentacular club. *b* and *c.* Side and front view of one of the large suckers.

Figs. 4—8.—Chiroteuthis Veranyi.

Fig. 4. Ventral view after opening the mantle cavity. *olf. org.* Spoon-shaped organ (olfactory). *n. gland.* Nidimental gland. *a. n. gl.* Accessory nidimental gland. *rect.* Rectum. *r. pap.* Renal papilla.

Fig. 5. After opening the renal sac and the funnel. *r. p.* Renal papilla. *v. p. a.* Viscero-pericardial aperture. *b. v. n.* Branch of visceral nerve. *a. n. gl.* Accessory nidimental gland. *nid. gl.* Nidimental gland. Cartilaginous socket and tooth of mantle fastening. *br. heart.* Branchial heart.

Fig. 6. The pericardium (*p. c.*) laid open. *v. p. a.* Viscero-pericardial aperture. *br. v.* Branchial vein. *br. h.* Branchial heart (in its portion of the pericardium). *ov.* Oviduct. *ventr.* Ventricle.

Fig. 7. The perigonadial portion of the cœlom laid open, as also the anterior renal chamber (*ar.*) containing its renal mass. *br. v.* Branchial vessels (vein and artery). *ext. ap.* External aperture of oviduct. *o. gl.* Oviducal gland. *int. ap.* Internal aperture of oviduct. *cæ.* Cæcum to intestine. *lig.* Ligament forming posterior attachment of ovary to the wall of cœlom, the position of the left oviduct indicated by dotted lines. *a. nid. gl.* Accessory nidimental gland. *v. p. a.* Viscero-pericardial aperture. *br. v.* Entrance of branchial vein.

Fig. 8. Nidimental gland of Chiroteuthis.

PLATE IX.

FIGS. 1—9.—Doratopsis vermicularis.

Figs. 1—3. Drawn by Miss Stone. Ventral (1), dorsal (2), and lateral (3) views. *tent.* Tentacular arms. *stell. org.* Stellate organs. *olf. org.* Olfactory organ. *nuchal cart.* Nuchal cartilage.

Fig. 4. View of oral surface. *p. lip.* Papillate lip. *b. memb.* Buccal membrane. *t.* Tentacular arm. IV. Fourth pair of arms with single row of suckers.

Fig. 5. View of interior of mantle cavity. *m. f.* Mantle fastening. *r. p.* Renal papilla. *p. vein.* Posterior renal vein. *g. gl.* Genital gland.

Fig. 6. Portion of neck region (dorsal), showing the stellate organs, *st. org.* *v. n.* visceral nerves, aorta, and *a. c.* alimentary canal.

Fig. 7. Tentacular club.

Fig. 8. Funnel opened along median line, showing valve, lateral pads of Verrill's organ, vena cava (*v. c.*), ink sac, and rectum.

Fig. 9. Ventral view of head region showing the olfactory organs. IV. Fourth pair of arms. *tent.* Tentacular arms.

PLATE X.

FIGS. 1—4.—Tracheloteuthis Behnii.

Fig. 1. Dorsal view. *p. p.* Pigmented patches. II, III. Second and third arms, with larger suckers.

Fig. 2. Ventral view after opening the mantle. *o. o.* Olfactory organ supplied by nerve (*n.*). *m. f.* Mantle fastening. *m. d. i.* Musculi depressores infundibuli. *v. c.* Vena cava. *r.* Kidneys. *rect.* Rectum. *c.* Ridge, cartilaginous ridge for mantle fastening.

Fig. 3. Tentacular club, with lateral protective membrane (*l. m.*).

Fig. 4. Funnel, opened to show valve and median papilla (*m. p.*) and lateral pads (*l. p.*) of Verrill's organ. *c. groove.* Cartilaginous groove for mantle fastening.

FIGS. 5—7 show modifications of the olfactory organ (*o. o.*)—Histioteuthis, Loligo, and Thysanoteuthis. *t. c.* Anterior transverse crest. *t. c'.* Posterior transverse crest. *l. c.* Longitudinal crest. *e.* Eye.

FIGS. 8—12.—Histioteuthis Ruppelli.

Fig. 8. Renal chamber opened, showing *v. c.*, vena cava, and *h. d.*, hepatic ducts with renal appendages. *l. m.* Lateral renal masses on the renal veins. *ov. gl.* Oviducal gland. *rect.* Rectum. *br. heart.* Branchial heart. *r. p.* Renal papillæ. *v. p. s.* Viscero-pericardial aperture.

Fig. 9. Cœlom opened (pericardium and perigonadium). *v. p. a.* Viscero-pericardial aperture. *i. a.* Internal aperture of renal papilla. *st.* Stomach. *g. ar.* Genital artery. *ovd.* Oviduct. *int. ap.* Internal aperture of oviduct. *rt. ovd.* Right oviduct. *rect.* Rectum. *br. art.* Branchial artery. *br. heart.* Branchial heart.

Fig. 10. Funnel opened, showing valve and lateral pads of Verrill's organ. *m. f.* Mantle fastening.

Fig. 11. Mantle cavity laid open. *m. d. i.* Musculi depressores infundibuli. *ov. gl'.* Accessory oviducal gland. *gl.* Oviducal gland proper. *nid. gl.* Nidimental gland. *c.* Ridge, cartilaginous ridge fitting into the groove (*m. f.*) forming the mantle fastening.

Fig. 12. Tentacular arm, with pad and suckers forming the fixing apparatus.

Fig. 1.

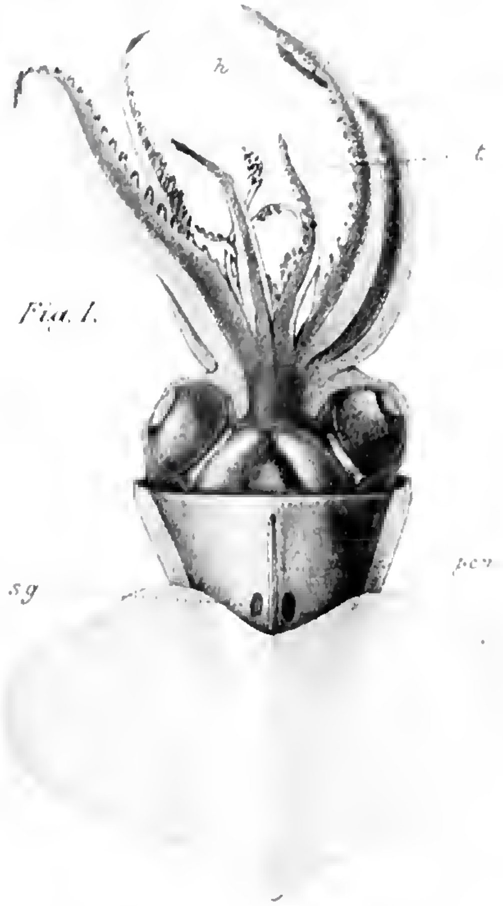
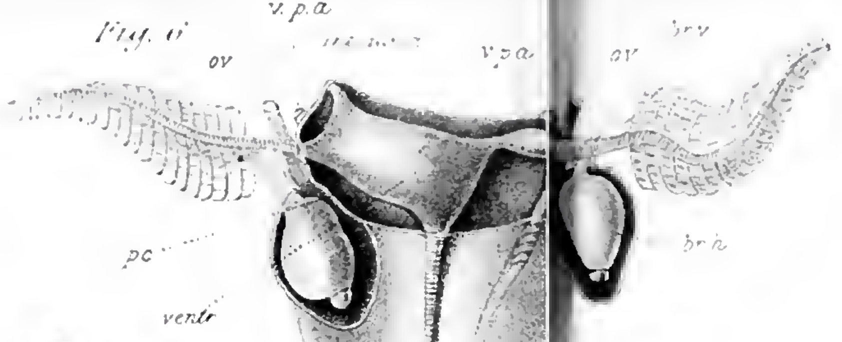


Fig. 6



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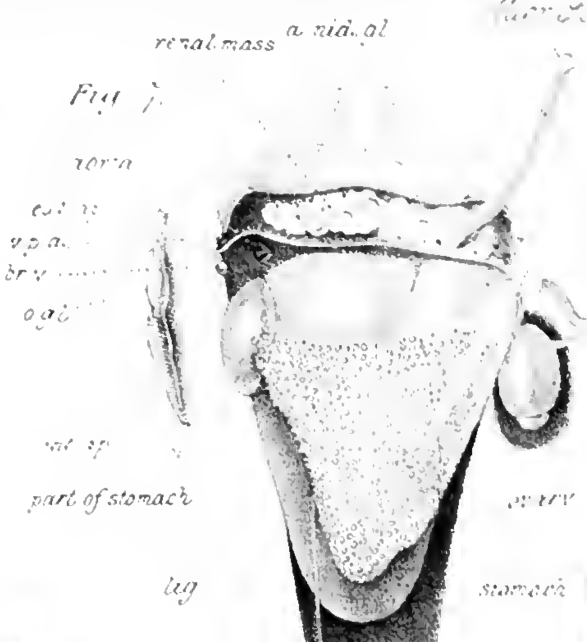
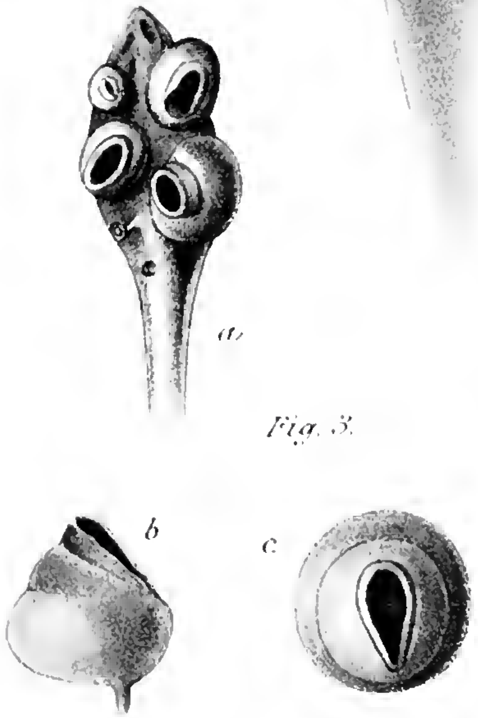


Fig. 3.



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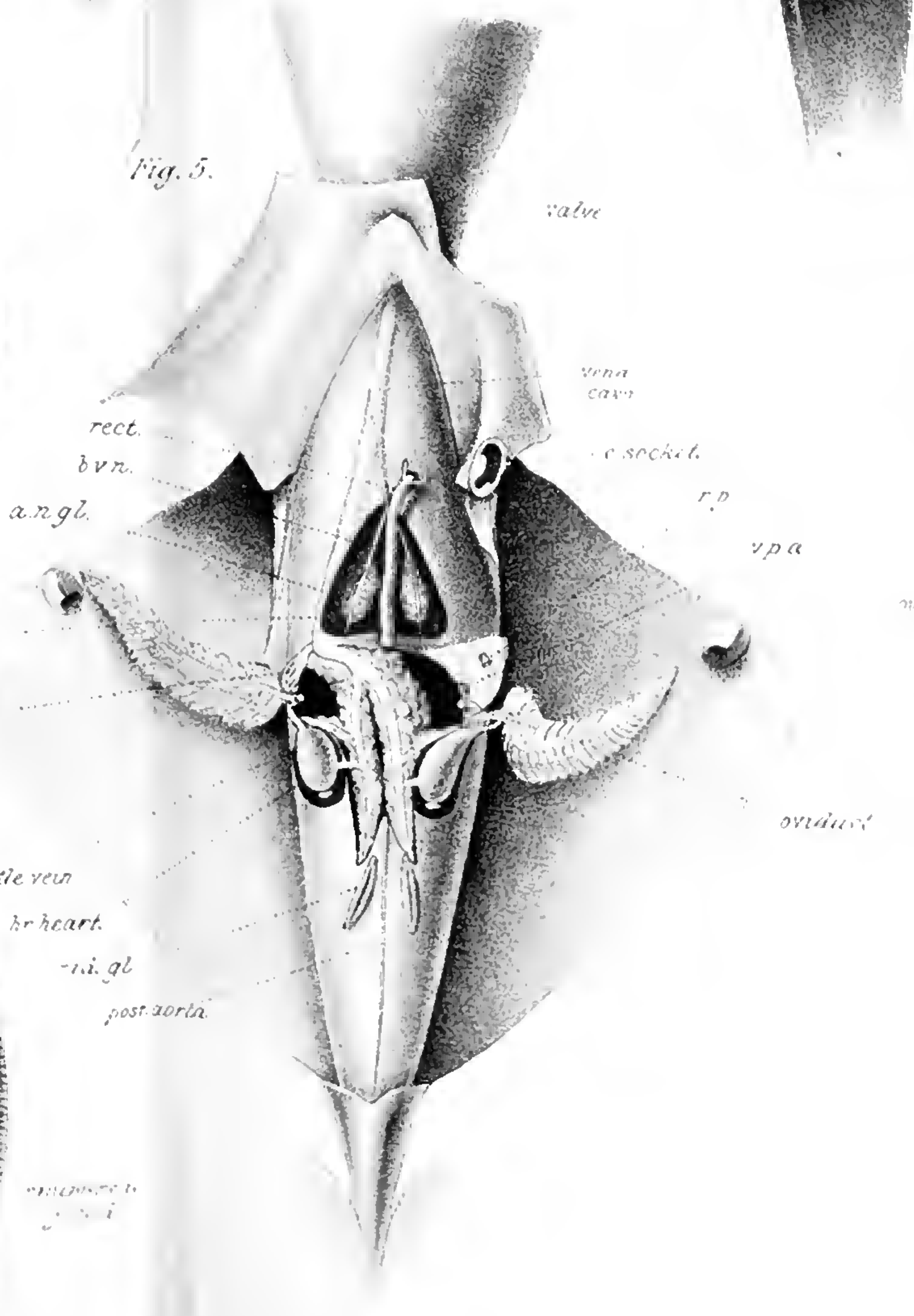


Fig. 4

Fig. 2

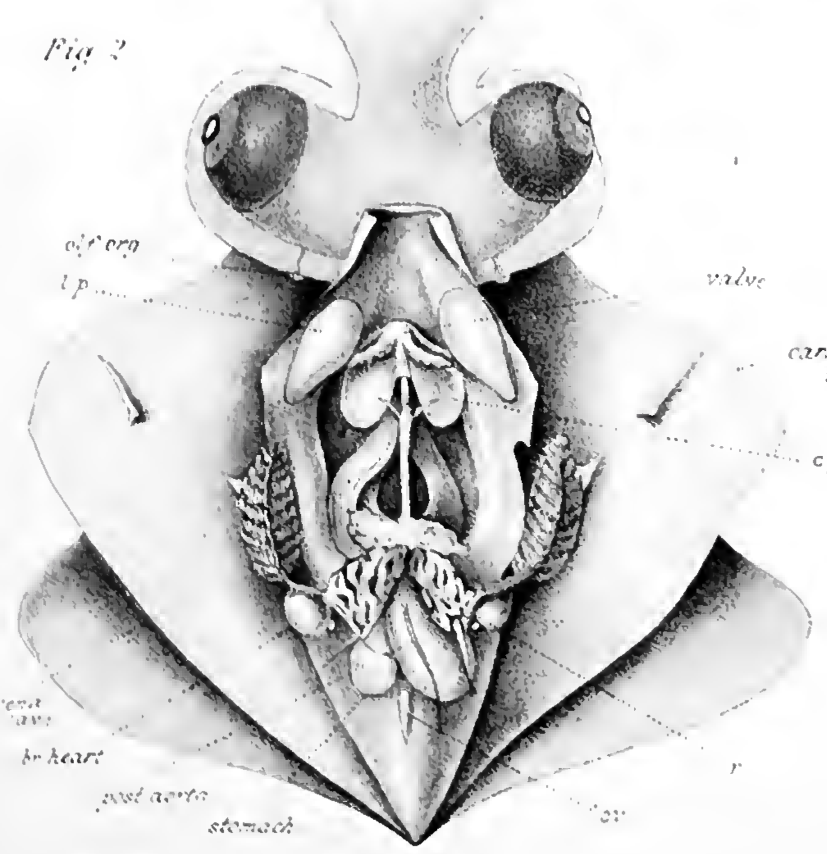
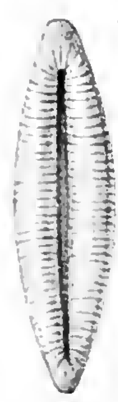


Fig. 8.



F. V. Weiss del.

P. Huth, Lith. Edin.

Figs 1-3, VÉRANIA SICULA.

Figs 4-8, CHIROTEUTHIS VERANYI.

Fig 1

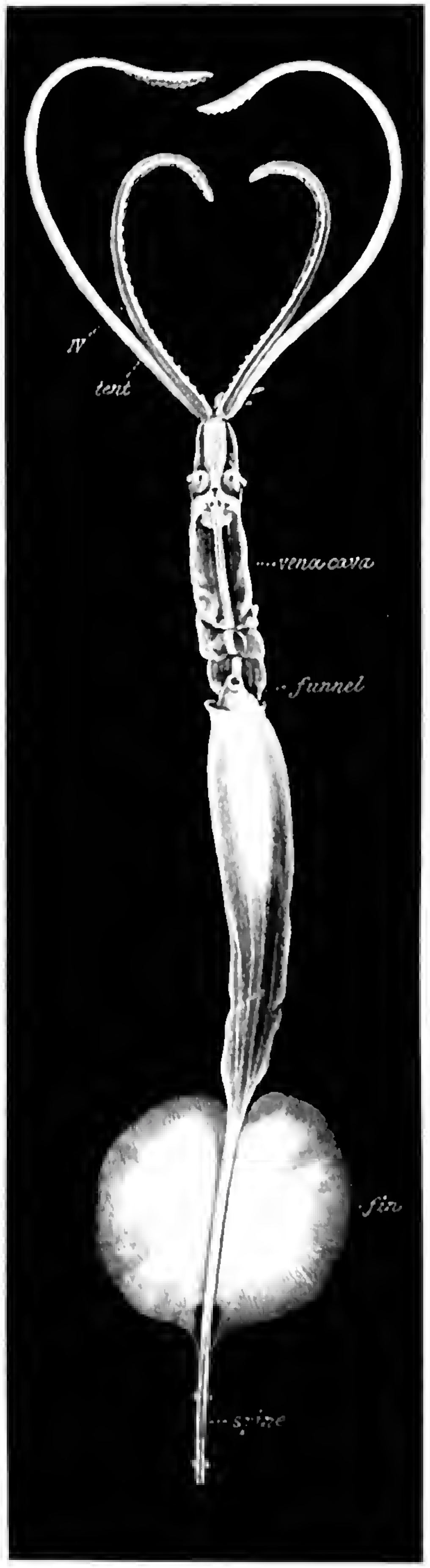


Fig. 2

Fig 3

Fig. 4

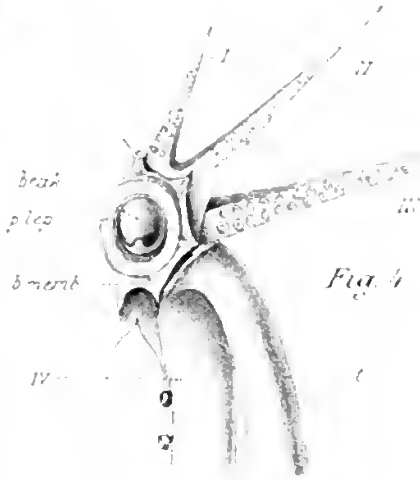


Fig. 5

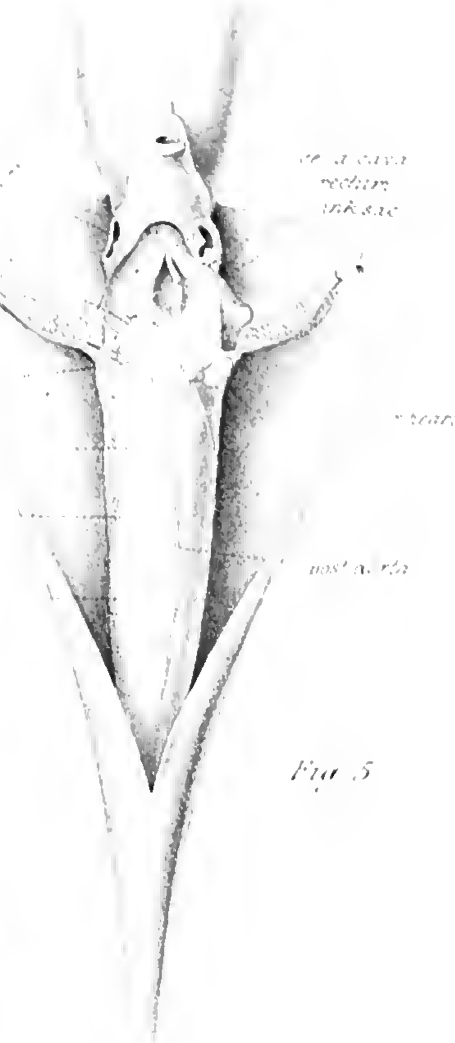


Fig. 9.

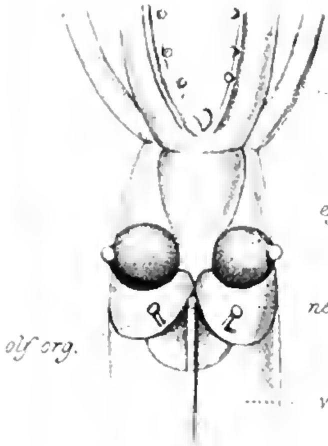


Fig 7.

Fig 6

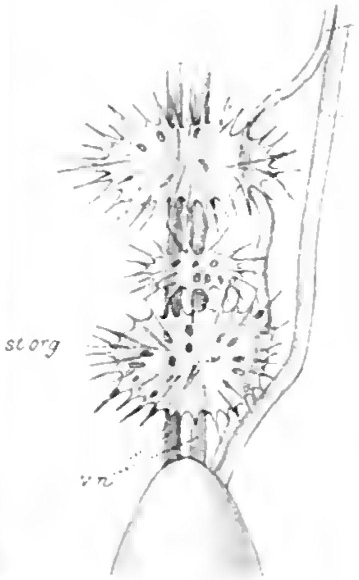


Fig 8.

Stone & Weiss del.

DORATOPSIS VERMICULARIS. (Rochebrune)

F. Huth Lith.r Edin.r

Fig. 1

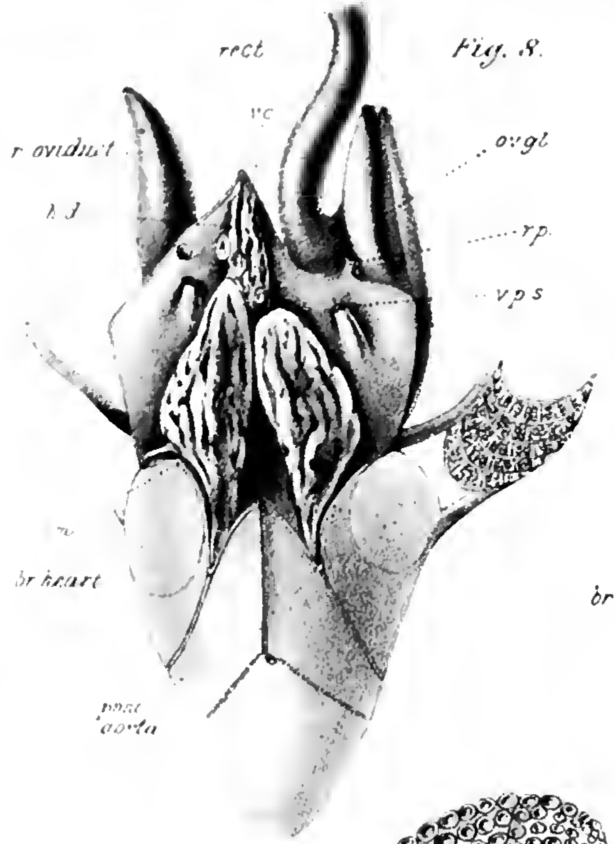


Fig. 8.

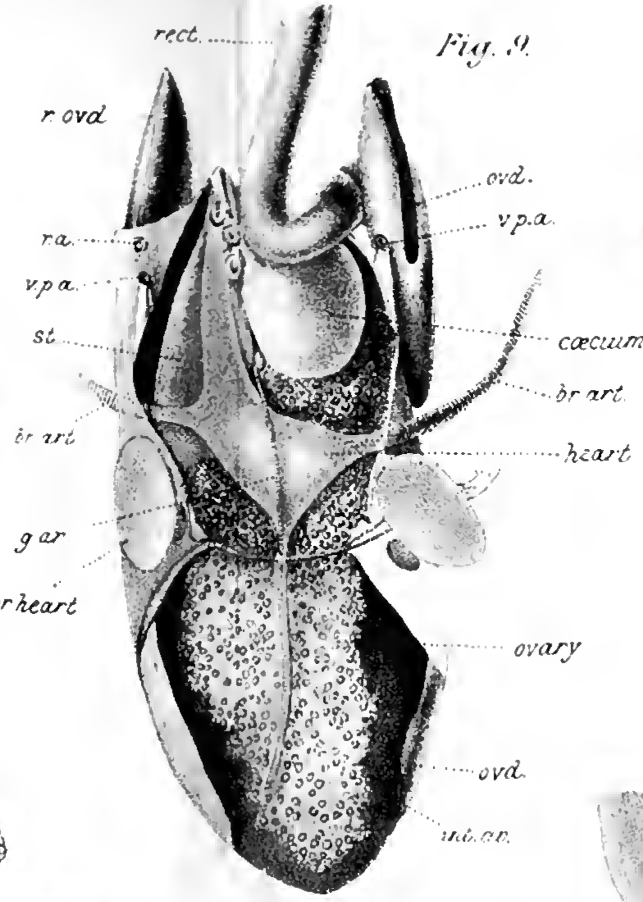


Fig. 9.

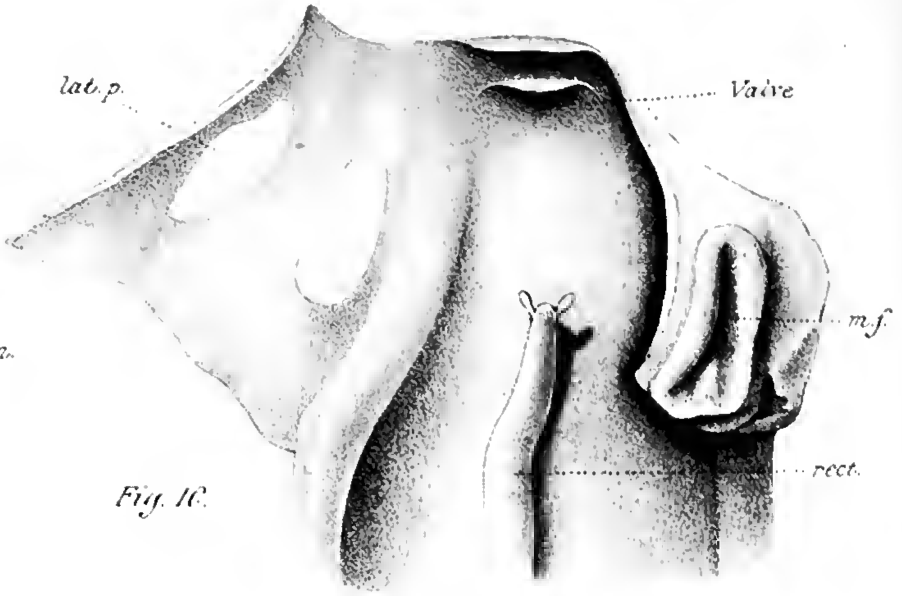


Fig. 10.

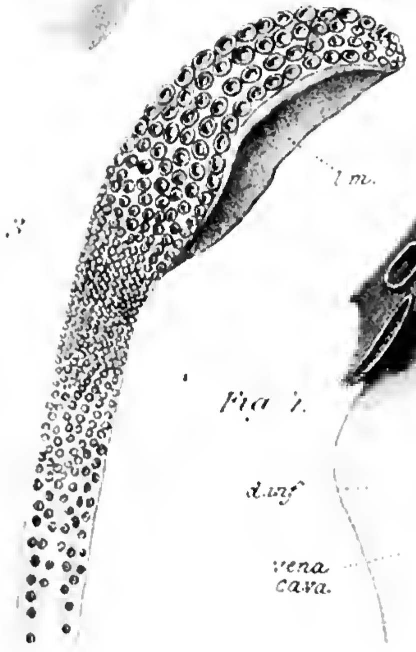


Fig. 3

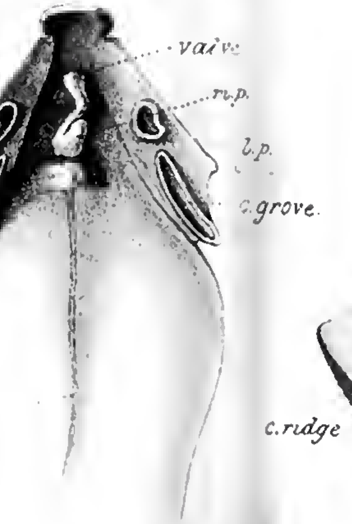


Fig. 4.

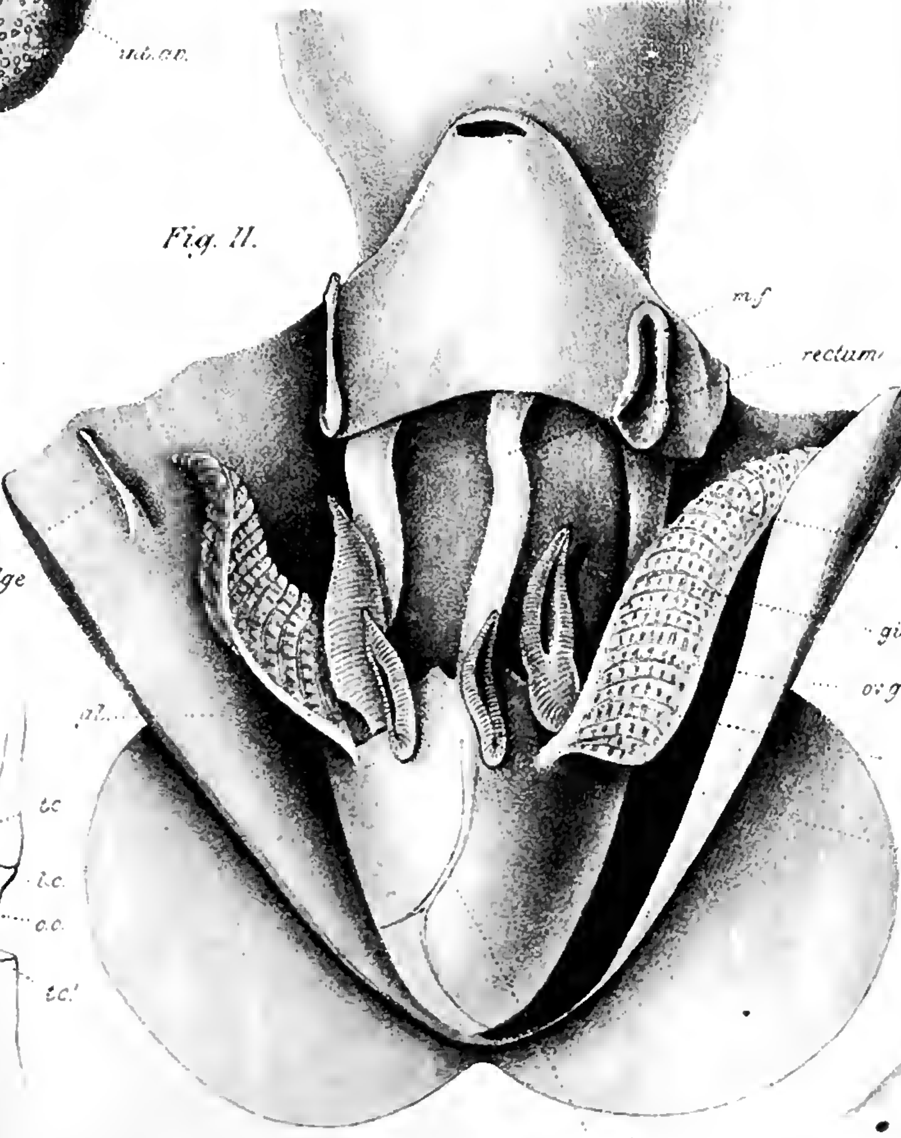


Fig. 11.

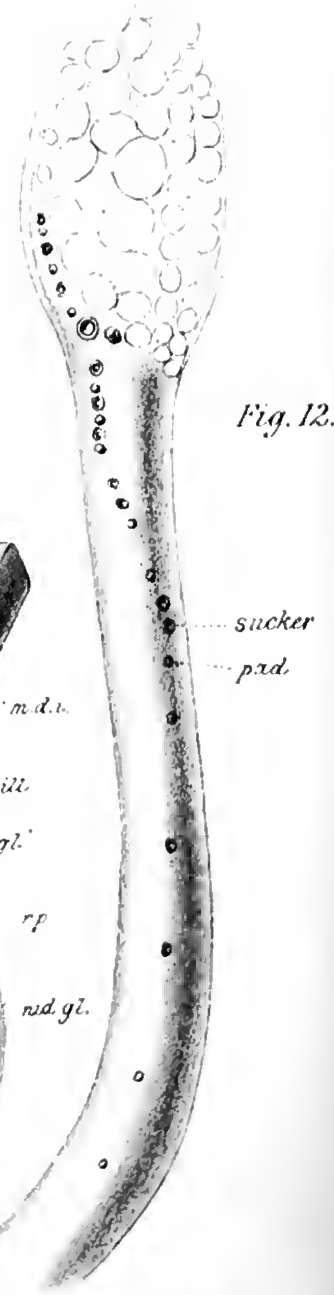


Fig. 12.

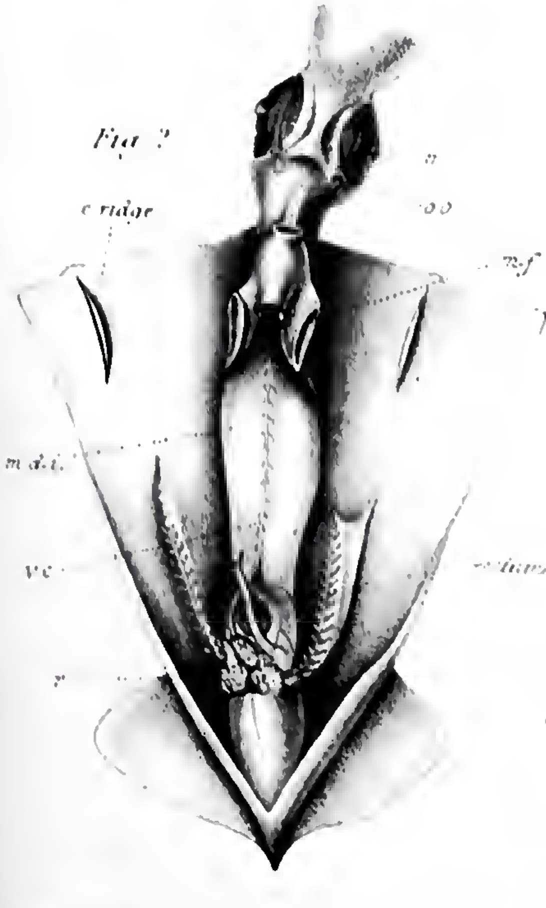


Fig. 2

Fig. 5.
HISTIOTEUTHIS.

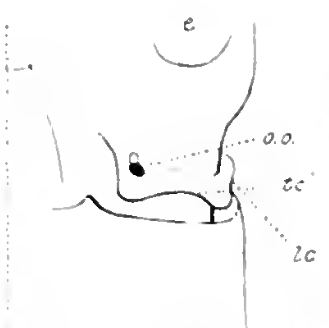


Fig. 6.
LOLIGO.

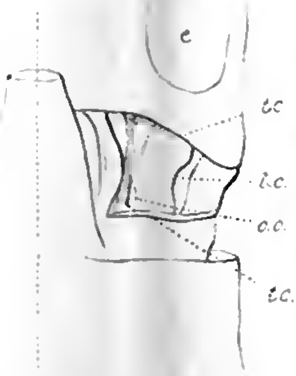


Fig. 7.
THYSANOTEUTHIS.

F. E. Weiss del.

Figs 1-4, TRACHELOTEUTHIS BEHNII.

P. Huth, Lith^r Edin^r

Figs 8-12, HISTIOTEUTHIS RUPPELLI.

The Organ of Verrill in Loligo.

By

Malcolm Laurie, B.Sc.
From the Zoological Laboratory of University College, London.

With Plate XI.

In a paper on North American Cephalopoda[1] Verrill describes a valve-like organ at the base of the siphon in Desmoteuthis and Taonia, in both of which genera the true valve is absent. His drawing of this structure in Desmoteuthis tenera is reproduced in fig. 1. It is there seen to be composed of a median portion, (*m.*) lying on the dorsal side of the siphon, and a pair of lateral cushions (*n. n′.*). The median portion is raised into three papillæ, one (*i.*) median and a pair (*i′.*) more posterior in position.

This structure to which the name of Verrill's organ has been given by Hoyle[2] has been observed in a few other species, but is by no means common. It is figured by Mr. Weiss in the present number of this Journal for several Oigopsidæ (see Pl. VIII, fig. 2; Pl. IX, fig. 8; Pl. X, fig. 10). I was therefore much interested to discover, in sections of a young Loligo about 6 mm. in length, made in Professor Lankester's laboratory at University College, London, a structure in the siphon which I think there is no doubt is Verrill's organ. The general appearance of this structure is shown in fig. 2. It consists of a median dorsal cushion, which is prolonged

[1] 'Trans. Conn. Acad.,' vol. v, part 2.

[2] 'Challenger Report,' vol. xvi.

backwards into two large processes, and a pair of lateral cushions on the ventral wall of the siphon. The dorsal cushion is produced forwards into a papilla which is best seen in section (fig. 6, *i.*). Figs. 3—6 show sections through the siphon and Verrill's organ. The valve (figs. 2 and 6, v.) is well developed, and quite distinct from Verrill's organ.

An examination of the histological structure shows the organ to be glandular. It is composed (fig. 7) of columnar goblet cells almost entirely filled with a clear transparent substance which stains very darkly with hæmatoxylin. The nuclei are at the bottom of the cells, and are surrounded by a small quantity of granular protoplasm. On the surface of the organ, more especially in the older specimens, there is a large quantity of mucus-like substance which has apparently been excreted from the cells. The organ of Verrill thus appears to be a mucus gland. It may, as Verrill suggests, function as a valve in those forms in which a true valve is wanting, but such a function would be secondary.

It is well developed in Ommastrephes in specimens about 8 mm. long. I can find no trace of it in the adults of either Loligo or Ommastrephes.

As regards its use to the organism or its homologies outside the Cephalopoda, I can say nothing. I think that Verrill has no foundation for his suggestion[1] that the dorsal cushion is "a true homologue of the foot of Gasteropods." Its presence, so largely developed in the young, seems to indicate that it is an archaic structure in the group of Cephalopoda, but there are no grounds for identifying it with any particular structure existing in Gastropods.

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[1] Loc. cit., footnote p. 432.

EXPLANATION OF PLATE XI,

Illustrating Mr. Malcolm Laurie's Paper on the "Organ of Verrill in Loligo."

List of Reference Letters.

s. Siphon. *m.* Mediodorsal cushion of Verrill's organ. *n. n'.* Lateral cushions. *i.* Central papilla. *i'.* Lateral papillæ. *p.* Mantle. *v. c. s.* Superior vena cava. v. Valve.

Fig. 1.—Siphon of Desmoteuthis tenera. Natural size. After Verrill.

Fig. 2.—Organ of Verrill in young Loligo. Dorsal cushion.

Fig. 2 *a.*—Ventral wall of Siphon, showing paired cushions.

Fig. 3.—Transverse section of young Loligo. $\times \frac{60}{1}$.

Fig. 4.—Transverse section of young Loligo further down than Fig. 3. $\times \frac{60}{1}$.

Fig. 5.—Longitudinal sagittal section of young Loligo to one side of the middle line. $\times \frac{60}{1}$.

Fig. 6.—Longitudinal sagittal section of young Loligo in middle line. $\times \frac{60}{1}$.

Fig. 7.—Section of part of the organ of Verrill in a young Loligo. $\times \frac{650}{1}$. *n.* Nuclei. *mu.* Mucus in the goblet cells. *mu'.* Mucus on surface of organ.

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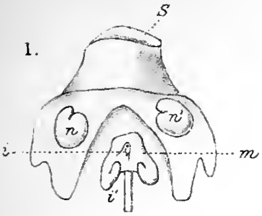

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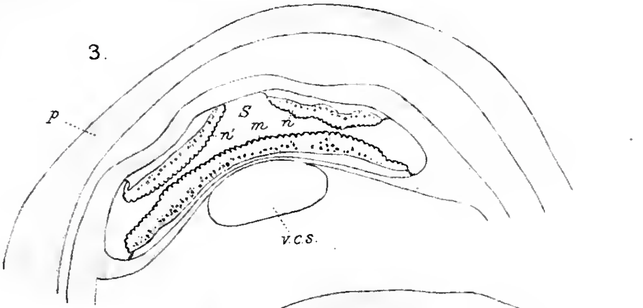

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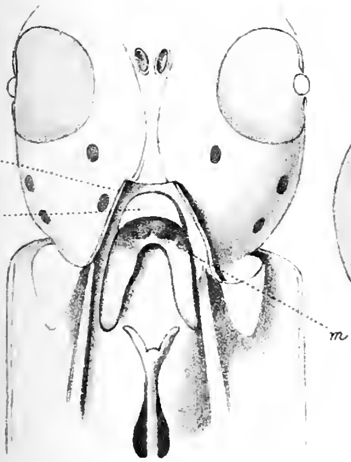

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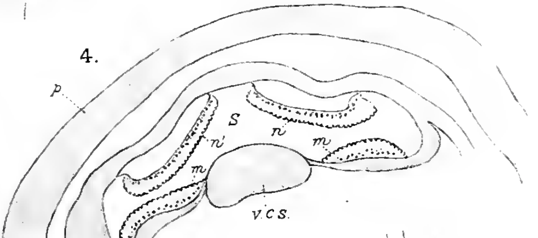

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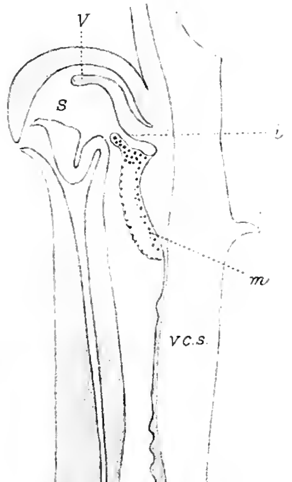

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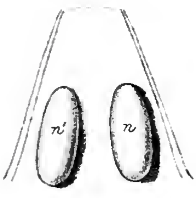

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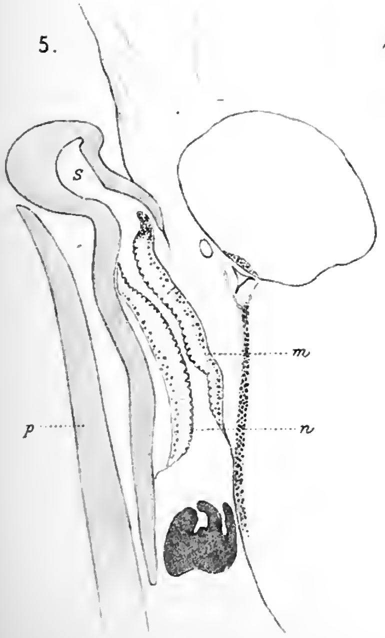

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M Laurie del

F. Huth, Lith^r Edin^r

ADDITIONAL LIST OF ERRATA IN MR. SEDGWICK'S MONOGRAPH OF THE GENUS PERIPATUS IN VOL. XXVIII OF THIS JOURNAL.

On page 439, twelfth line from bottom, for "Pl. I" read "Pl. XXXIV."

On page 441, fourteenth line from top, for "Pl. I" read "Pl. XXXIV."

On page 448, fifth line from bottom, for "6 mm." read "·6 mm."

On page 455, ninth and tenth lines from bottom, for "legs" read "pairs of legs."

On page 464, eleventh line from bottom, for "discernable" read "discernible."

On page 467, ninth line from bottom, for "twenty-nine and" read "twenty-nine pairs and." On the next line, for "legs" read "pairs of legs."

On page 468, sixth and tenth lines from top, for "legs" read "pairs of legs."

On page 468, twelfth line from top, for "twenty-three" read "thirty-three."

On page 468, tenth, eighth, and sixth lines from bottom, and on the last line, for "legs" read "pairs of legs."

On page 471, seventeenth, nineteenth, and twenty-first lines from top, for "legs" read "pairs of legs."

On page 474, eighteenth line from top, for "higher" read "lighter."

On page 476, ninth line from top, for "fig. 27" read "fig. 29."

On the Structure of Three New Species of Earthworms, with Remarks on Certain Points in the Morphology of the Oligochæta.

By

Frank E. Beddard, M.A.,
Prosector of the Zoological Society, Lecturer on Biology at Guy's Hospital.

With Plates XII and XIII.

This paper contains (1) an anatomical description of three new species of Earthworms, of which two are from New Zealand; (2) a discussion of certain points in the structure of the Oligochæta generally, which have been suggested by the study of these forms, but which involve the partial description of other Earthworms not systematically treated here.

The New Zealand Earthworms I owe to the kindness of Mr. W. W. Smith, of Ashburton, New Zealand, who sent me a large number of well-preserved examples from different localities, as well as a few living specimens. I also desire to express my thanks to Sir Walter Buller, K.C.M.G., who asked Mr. Smith to procure me some specimens.

Typhæus Gammii comes from Darjeeling; a number of examples were kindly collected for me by Mr. G. A. Gammie, a member of the Chinchona Cultivation Staff. They were transmitted to me with a number of Perichæta from the neighbourhood of Calcutta, by Drs. King and Bain, of the Seebpore Botanical Gardens, whom I desire to take this opportunity of thanking. My thanks are also tendered to Dr. John Anderson, F.R.S., at whose request the specimens were collected and forwarded to me.

Acanthodrilus annectens, n. sp.

This species combines to a certain degree the characters of two other New Zealand Acanthodrili recently described by me (1), viz. A. multiporus and A. novæ-zealandiæ; not, however, to so marked an extent as might lead one to infer the possibility of its being a hybrid.

It is a comparatively small worm, measuring about 3 inches in length. The colour of the living worm is "pink, or white and pink."

EXTERNAL CHARACTERS.

The setæ are paired, the individual setæ being at some little distance from each other.

The Clitellum occupies segments 13—20 (inclusive); the glandular modification of the epidermis is not developed on the ventral surface, as is usual in this genus.

The anterior end of the body is somewhat swollen, and the segments here are somewhat difficult to map owing to the division of the segments into numerous annuli. In these particulars the present species agrees very closely with A. multiporus.

The atrial pores are upon the seventeenth and nineteenth segments, and correspond in position to the outermost of the ventral pair of setæ. They are placed upon the summits of prominent papillæ; the two pores of each side are connected by a groove. In one specimen the pore of the vasa deferentia was visible upon the eighteenth segment. As a rule these pores are invisible.

The oviducal pores are paired, and lie upon the fourteenth segment; each is placed in front of, and a little to the inside of, the ventralmost seta of the ventral pair.

The spermathecal pores are in the furrows separating segments 7—8 and 8—9; they correspond in position to the atrial pores.

The nephridiopores are visible in most of the segments of the body; they lie in front of the outermost seta of the outer pair.

INTERNAL ANATOMY.

Reproductive Organs.—The most remarkable fact about the reproductive organs of this species is illustrated in Pl. XII, fig. 13; that is, that the testes (*t.*) and ovaries (*ov.*) instead of being situated on the anterior wall of their respective segments are placed upon the posterior wall in close proximity to the funnels (*f. ov.*). I should have been disposed to regard this arrangement as abnormal had it not been for the fact that it occurred in all of the two or three specimens studied by me.

The vesiculæ seminales of this species are like those of other Acanthodrilus in their racemose character, and in the fact that they do not envelop the funnels of the vasa deferentia. It may easily be seen in longitudinal sections of the worm that the vesiculæ, although so different in outward appearance from those of Lumbricus, only differ really in being branched instead of simple outgrowths (see Bergh **8**, fig. 13, *v. s.*^{4}) of the septa.

The atria, as is always the case with Acanthodrilus, are two pairs situated in the seventeenth and nineteenth segments. The vasa deferentia, as also appears to be the rule in this genus, open quite independently of the atria upon the eighteenth segment (Pl. XIII, fig. 12). The two vasa deferentia unite just before their external orifice (♂), which is situated just on the boundary line between the seventeenth and eighteenth segments; the pores are also situated in a groove which connects the two atrial pores of each side, and the presence of which is highly characteristic of the genus Acanthodrilus as also of Deinodrilus (see Pl. XIII, fig. 3). The two vasa deferentia run side by side and obliquely, through the muscular layers of the integument to the external pores, crossing on their way the duct of the atrium of the seventeenth segment (*p.*). In longitudinal sections I traced the vasa deferentia back to the thirteenth segment, running in the longitudinal muscular layer and at some distance from the surface, nearly midway between the two surfaces of the longitudinal muscular layer; after this they gradually approach the peritoneal face

External Characters.

The length of the largest specimen is about five inches. The arrangement of the seta is shown in fig. 9 of Pl. XIII. A prostomium is present (Pl. XIII, fig. 4), but does not completely divide the circumoral segment. The clitellum is well developed in one of the two specimens which I examined; it occupies segments 14, 15, and 16, having therefore precisely the range which characterises so many species of Perichæta; as in that genus the glandular modification of the epidermis of the clitellar segments is continuous right round the body, being equally well developed upon the ventral and upon the dorsal surface (Pl. XIII, fig. 3, *cl.*).

The only apertures visible upon the outside of the body (see Pl. XIII, fig. 3) are the dorsal pores, the apertures of the male and female reproductive ducts, and of the spermathecæ. No nephridiopores could be made out. The dorsal pores commence between the 11th and 12th segments. The oviducal pores are upon the fourteenth segment; they are paired and situated a little in front and to the inside of the ventralmost seta.

The apertures of the atria are, as in Acanthodrilus, two pairs: one pair are upon the seventeenth, the other upon the nineteenth segment; they correspond in position to the outer seta of the ventral pair. The spermathecal pores are close to the anterior border of segments 8 and 9; they correspond in their relation to the setæ with the male pores.

Internal Anatomy.

Integument.—Pl. XIII, fig. 10, illustrates a section through the body wall, in the hinder region of the worm. The section has been drawn with the aid of a camera lucida, and therefore indicates correctly the relative thickness of the different layers, which together constitute the body wall. As appears to be almost always the case, the longitudinal muscles are much thicker than the circular; in this worm they are about six times as thick.

The longitudinal muscles have their fibres arranged in that remarkable bipinnate fashion which is found in many species of Lumbricus and Allolobophora, but is comparatively rare elsewhere.

With regard to the vascular system, the only facts which I am able to record are, (1) the condition of the dorsal vessel; (2) the number and connections of the "hearts."

The dorsal vessel is a completely double tube, with the exception of that portion which lies in the first four or five segments. It resembles the dorsal vessel of Acanthodrilus multiporus in the fact that the two tubes are perfectly separate throughout, except where they become permanently fused at the anterior extremity of the body. The somewhat contracted condition of the worm frequently caused the two halves of the dorsal vessel to become widely separate in the middle of each segment, while at the mesenteries they come into close relation; there is, however, no fusion of the two tubes at these points, such as occurs in A. novæ zealandiæ and Microchæta. I observed six pairs of lateral "hearts," the last pair being in segment 13: the last four pairs are specially large, and are connected with the supra-intestinal as well as with the dorsal vessels. The anterior two pairs (there are probably one or two pairs in addition to those which I have mentioned) are much more slender and only connected above with the dorsal vessels.

Septa. — The septa separating segments 8—9, 9—10, 10—11, 11—12, 12—13, are thicker than the rest, but not to so marked a degree as is often met with in Earthworms.

Alimentary Tube.—The pharynx has the usual characters. The gizzard lies in segments 6 and 7; the œsophagus is thick walled and highly vascular, but there appeared to be no distinct calciferous glands.

The intestine has a typhlosole (Pl. XIII, fig. 8).

The nephridia are not obvious on dissection except in segments 2, 3, and 4; in each of these segments is a tuft of nephridial tubules of considerable size; in the posterior segments nephridia are present, and open on to the exterior by several pores in each segment. The nephridial system of this worm is in fact like that of Acanthodrilus multiporus. I have not as yet worked it out in detail; this I hope to do later.

Cœlom.—It is the rule among the higher Oligochæta that the cœlom is a spacious cavity divided into a series of chambers by the transverse septa; only in the first few segments of the body is this arrangement interfered with by the development of strands of muscular fibres uniting the pharynx with the parictes. In these segments the cœlom forms an irregular system of lacunæ. Furthermore, the saccular outgrowths of the septa in the genital segments which envelope the testicular products, and sometimes also include the testes, the vasa deferentia funnels, and part of the ventral blood-vessel and nerve-cord, may be looked upon as specialised parts of the cœlom. Lastly, in Eudrilus there is a "perigonadial" space surrounding the ovary.

In Deinodrilus the dorsal blood-vessel is surrounded by a special cœlomic space in a way that is, at present, unique among Earthworms. This space does not appear to exist in the first fifteen segments; after this point the two dorsal blood-vessels are not as plainly visible on a dissection of the worm as they are anteriorly; the red colour of the blood is masked by the whitish colour of the tissues which form the walls of the perihæmal space. The fact that the blood-vessels are so clearly seen on dissection in the anterior segments, leads me to infer that here there is no perihæmal cœlomic space; but I am unable to support this view by a description of the microscopical appearance of the dorsal vessels in this region of the body, which I have not investigated by sections.

Pl. XIII, fig. 7, is a longitudinal section through one of the two dorsal vessels; and Pl. XIII, fig. 6, is a transverse section of the dorsal vessels more highly magnified.

It will be seen from these figures that the blood-vessels are surrounded by a widish tube which is further divided into two, one for each of the paired vessels.

The walls of this perihæmal space consist of a thin layer of fibres which are covered on both sides by peritoneal epithelium. The outermost epithelium consists of delicate flattened cells (fig. 6, *p.*); the perihæmal space is lined by rounded cells which are aggregated here and there into clumps (fig. 6, *p.*). I was at first inclined to regard these cells as free corpuscles which had become adherent to the walls of the perihæmal space; the fact, however, that these cells were invariably, so far as my experience goes, attached to the periphery of the perihæmal space, not to the periphery of the contained blood-vessel, seemed to show that they are the peritoneal lining of this section of the cœlom. It seems certain that the cells are in a state of energetic proliferation, and it is possible that in this perihæmal space—and from its lining cells—is carried on the formation of the cœlomic corpuscles. The blood-vessels themselves are covered by a single layer of large cells (*p″.*) filled with yellowish-brown granules. Some of these cells appeared to be multinucleate, and there is some variation in size.

The enclosure of the dorsal blood-vessel in a special cœlomic sac suggests of course the pericardium of higher types, and in any case it may be compared with the condition of the cœlom in the Hirudinea, where the principal blood-vessels as well as other organs are often included in separate cœlomic spaces. Among the Chætopoda also a commencement of a secondary subdivision of the cœlom is to be seen. In the Capitellidæ a series of longitudinal chambers enclose the nephridia and other organs; but I am not aware that hitherto anything of the kind has been described in the Oligochæta.

Reproductive Organs.—The vesiculæ seminales occupy segments 11 and 12; they are racemose organs like those of Acanthodrilus. The testes I have not seen.

The vasa deferentia open by funnels in segments 10 and 11; the funnels of segment 11 are quite independent of the vesicula. I could not trace the course of the vasa deferentia; but in all probability they open, as in Acanthodrilus, upon the eighteenth segment.

The atria are in segments 17 and 19; the external apertures of these organs have been already mentioned. The atria themselves are so exactly like those of Acanthodrilus that no further description is necessary.

The ovaries are situated on the anterior wall of segment 13; they are digitate bodies like the ovaries of Acanthodrilus.

The oviducts open by funnels which are placed near to each other and on either side of the nerve-cord, on the posterior wall of segment 13. The external pores, as already stated, are upon the 14th segment.

The spermathecæ have a very characteristic form, which is illustrated in Pl. XIII, fig. 5. The spermatheca is a somewhat oval pouch, which suddenly narrows into a slender duct, opening close to the anterior margin of the segment. At the junction of the pouch with the duct are three diverticula, two on one side and one on the other; the diverticula are very much smaller than the pouch, and of a regular oval form.

The following table indicates the principal points in which Deinodrilus agrees with Acanthodrilus or Perichæta:

	Acanthodrilus.	Deinodrilus.	Perichæta.
Clitellum .	Segments 12—19, or thereabouts; undeveloped between the atrial pores and the corresponding area on the other segments.	Segments 14—16 (inclusive); continuous all round the body.	Usually segments 14—16 (inclusive); continuous all round the body.
Setæ . .	8 per segment.	12 per segment.	20—100 per segment.
Atria . .	Two pairs of convoluted tubes opening on to segments 17 and 19.	Two pairs of convoluted tubes opening on to segments 17 and 19.	Usually represented by a single pair of branched glands opening on to eighteenth segment.[1]

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[1] In Bourne's P. Stuarti (9) the atria appear to be like those of Acanthodrilus.

Typhæus Gammii, n. sp.

The largest specimen measured about 10 inches in length (it is considerably contracted), and between a quarter and half an inch in thickness at the head end.

External Characters.

As in T. orientalis there is no prostomium, the mouth is therefore precisely terminal in position.

The setæ are disposed in pairs; the dorsal and ventral pair of one side are nearer together than the two ventral pairs; the interval which separates the latter is about one fourth to one fifth of the space which lies between the dorsal pairs of setæ.

The segmentation of the body is a little difficult to make out, owing to the fact that there are numerous furrows in addition to those which mark the limits of segments. The accompanying drawing (Pl. XII, fig. 7) illustrates the anterior segments of the body viewed from the ventral aspect.

The peristomial segment is occupied by numerous short, longitudinal creases, often of a zigzag form; these cease to exist some little way in front of the posterior end of the segment; there is, however, a fairly well-marked furrow, dividing this segment into two unequal halves. I am inclined to think that the two halves really correspond to two segments; the only objection to this is that there were no setæ discoverable upon the supposed second segment, which—at any rate in all other Earthworms—is the first seta-bearing segment. The assumption, however, that this is really a segment brings other organs of the body into positions more in accord with what is found in other Lumbricidæ. It will, therefore, be assumed that the area occupied by the longitudinal creases equals two segments.

The next two segments increase gradually in length, the last being marked with a faint transverse furrow. The number of furrows upon each of the following segments and their arrangement can be understood by the figure (Pl. XII, fig. 7). The segments of the clitellum possess no secondary furrows.

The clitellum occupies four segments—14 to 17 inclusive, and a portion of segment 13. In my earlier paper on the genus (2) an exactly similar condition of the clitellum is noted. Dorsal pores are present on all segments after, and including, the tenth. The pores of the spermathecæ are very conspicuous between segments 7 and 8; they correspond to the interval between the dorsal and ventral pairs of setæ (fig. 7, *c. p.*).

The male generative orifices are upon segment 17, and correspond to the ventral pair of setæ.

Between segments 19—20, 20—21, and occupying the whole of the space corresponding to the interval between the two ventral pairs of setæ, is a single large papilla (see fig. 3). The arrangement of the genital papillæ in this species is therefore apparently different from that which characterises T. orientalis. The number and position of the papilla agrees with Pontodrilus (Perrier (16), p. 177, pl. xiii, fig. 1, *b.*), with which genus, however, the present has but few other points in common.

INTERNAL ANATOMY.

Body Cavity.—Under this head I refer to the condition of the intersegmental septa in the anterior region of the body.

As in other Earthworms this species is seen to have a number of these septa thickened and hypertrophied. The first of these septa lies between the fourth and fifth segments; the next in the succeeding segment. The two following segments, which are occupied by the gizzard, are not divided by a mesentery at all unless the muscular bands which bind the anterior region of the gizzard to the body wall can be regarded as the remains of the septum dividing segment 6 from 7. Farther back are three thickened septa which lie between segments 8, 9, and 10. These latter are remarkable from the fact that they do not divide the body cavity into segments precisely equivalent to those indicated by the external characters.

The first of these mesenteries corresponds to the first furrow upon segment 9; the second is situated a little anterior to the boundary line between this and segment 10; the third is placed a little behind the first furrow of segment 10. It seems to me probable that these septa are those which should separate segments 8, 9, 10; but so little do they correspond to the external divisions of the segments in question, that the space enclosed by the two last septa, which should correspond to segment 10, actually has no setæ. The setæ of this segment occur behind the septum, and therefore, so far as the septa are concerned, in segment 11. The presence of a pair of transverse vascular trunks between each of these mesenteries is, however, a conclusive proof that they enclose two segments (see description of vesicula seminale, p. 114).

§ Vascular System.—As in the majority of Lumbricidæ, there is a dorsal vessel, a supra-intestinal, a ventral vessel, and two lateral trunks. The dorsal and ventral vessels communicate in segments 8, 9, and 10, by a pair of transverse vessels, a pair to each segment. In the two following segments are two pairs of stouter transverse vessels, which also communicate with the supra-intestinal vessel (Pl. XII, fig. 6).

The lateral trunks are very conspicuous in the gizzard segments. At each end of the gizzard they give off a system of branches, which supply it with blood; behind the gizzard the two lateral trunks run beneath the intestine, and each approaches very closely its fellow. I am unable to state how the lateral trunks originate.

§ Nephridia.—The nephridia of this species consist of innumerable delicate tubules, which are chiefly developed in the anterior segments of the body; they are at any rate more conspicuous here than elsewhere. As in T. orientalis, there is a special mass of these tubules in the first and second segments of the body. The characters of the nephridia in this genus resemble those of Perichæta, Acanthodrilus multiporus, Trigaster, &c., so far as the naked-eye appearances are concerned. I have ascertained by cutting sections of a portion of the integument in the region of, and including the orifice of a spermatheca, that in this part of the body, at any rate, there is more than a single pair of nephridial orifices to each segment. It is probably also the case in other parts of the body, but I am not able to give any accurate description of the arrangement of the external pores.

I am inclined to think that in all Earthworms when the nephridia have the characters recorded in this species, that is to say, where they consist of abundant scattered tufts of minute tubules, it will be discovered that the external apertures agree with those of Acanthodrilus multiporus, Dichogaster, and the present species (Beddard 5).

§ Alimentary Tract.—The gizzard is situated in the sixth and seventh segments. As is generally the case when this organ occupies two segments, the mesentery that should separate these segments is absent, or at most represented by rudiments. In the present species, as has been already said (p. 112), there are two muscular bands of a strap-like form by which the gizzard is attached to the body wall.

This species has a single pair of calciferous glands, which are situated in the twelfth segment (fig. 8, *ca.*).

The alimentary canal presents only one other feature of interest, and that is the presence of intestinal glands already recorded in T. orientalis.

The glands are, however, not confined to this genus, since they exist in much greater numbers in Megascolex, and have also been described by Horst in Acanthodrilus, and by myself in Eudrilus.

In Typhæus the glands agree in their minute structure (Pl. XII, fig. 2) with those of Megascolex, but differ anatomically in the fact that the two glands of each pair become fused together on the middle dorsal line of the intestine, and also in the fact that the glands of consecutive segments are connected. The minute structure bears a very close resemblance to that of the calciferous glands.

§ Reproductive System.—This worm differs from the greater number of Lumbricidæ in the possession of only a single pair of testes and a single pair of vesiculæ seminales corresponding to them. The vesiculæ seminales (which are of course the "testes" of my former paper on Typhæus) are long and tongue shaped, and extend back on either side of the œsophagus as far as the male pore, i. e. to the seventeenth segment; they commence in the tenth segment, and therefore occupy seven segments. The surface of the vesiculæ is not plain and smooth, but projects into numerous irregular rounded clusters. At the anterior extremity the vesiculæ become attached to the last thick septum, and just below their attachment is a small cavity, which contains the testes and the funnels of the vasa deferentia (Pl. XII, fig. 1, *a.*). This is to be regarded, I imagine, as a median unpaired portion of the vesiculæ which so often occurs in Earthworms.

This compartment contained a mass of spermatozoa; it is not divided up by trabeculæ, as are the paired portions of the vesiculæ, except for two fibrous bands which pass up to the mesentery. The innermost pair of setæ of the tenth segment (see above, p. 112) are enclosed within this compartment.

The testes are contained within this compartment; they are a pair of round bodies (fig. 1, T.), which have very much the appearance of a woollen button.

The single pair of vasa deferentia funnels (*f.*) are also contained within this compartment; each is situated exactly opposite to its own testis.

The vas deferens of either side passes down to the seventeenth segment, where it opens on to the exterior near to the atrium and a bundle of penial setæ, as in T. orientalis (Pl. XII, fig. 1).

Perhaps the most remarkable fact in the anatomy of this worm is the peculiar relation that exists between the atrium and the vas deferens. These two structures in other Earthworms open together by a common duct. In Typhæus, however (fig. 1), the vas deferens, which becomes a little wider at its termination, enters the body wall independently of the atrium and behind it. A series of transverse sections through this part of the body show that the vas deferens does ultimately join the atrium, though only just beneath the epidermis. The vas deferens is ciliated up to the point where it perforates the tissues of the body wall. After this the epithelial cells which line the vas deferens lose their cilia. The sac containing the penial setæ (Pl. XIII, fig. 1) is a diverticulum of the atrium (Pl. XII, fig. 5, *g.*), just before the junction of the latter with the vas deferens. These facts are not only of interest as being unique among Earthworms, and as forming a distinguishing feature of the genus Typhæus, but also from the point of view of a comparison with another Oligochæt—Ocncrodrilus (see p. 125).

The ovary is situated in the thirteenth segment (fig. 9, *ov.*).

The oviduct is also similar in structure and position to that of other Lumbricidæ; it opens on to the exterior in front of the ventralmost seta of the ventral pair (Pl. XII, fig. 9, *od.*).

The spermathecæ are situated in the eighth segment, and open, as already said, on the boundary line between this segment and the one in front. Each spermatheca consists of a large thin-walled pouch, and a small diverticulum on each side, which is composed of a number of separate diverticula united within a common muscular sheath.

The above account of the anatomy of Typhæus seems to indicate a general resemblance in structure to T. orientalis, coupled with certain differences which appear to me to be on the whole sufficient to warrant the specific separation of the two forms.

The genital papillæ are more numerous in T. orientalis than in the present species; it is true that this character has to be used with caution in the discrimination of species, but in the species under discussion which is represented by fully mature individuals, the differences are so great that I cannot but regard them as of specific value. The genital seta (cf. Pl. XIII, figs. 1, 2) are distinctively different in the two species. The vas deferens in T. Gammii enters the body wall independently of the atrium; in T. orientalis, as in other Earthworms, the vas deferens joins the muscular portion of the atrium.[1]

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[1] I mention this supposed difference with some hesitation, not having the specimens of T. orientalis at hand to refer to.

TYPHÆUS.

Generic Definition.—Setæ paired and confined to the ventral half of the body; dorsal pores present; clitellum developed upon segments 13—17. Male genital pores (intraclitellian) upon seventeenth segment corresponding with ventral pair of setæ. A single pair of spermathecæ, each furnished with two trifid diverticula, opening between segments 7 and 8 on a line with interspace between dorsal and ventral pairs of setæ. A single pair of testes in segment 10; a single pair of vesiculæ seminales enclosing testes and funnels of vasa deferentia, and reaching back for three or four segments. A single pair of vasa deferentia, each opening in common with, or close to, a coiled tubular atrium like that of Acanthodrilus; penial setæ present. Ovaries and oviducts occupying the usual position in the thirteenth and fourteenth segments; gizzard single, intestine furnished with six or seven pairs of glands on the dorsal surface. Nephridia forming inconspicuous tufts, nephridiopores of each segment numerous.

T. Gammii.—Penial seta with wavy ridges round distal portion. Genital papillæ two, on boundary line between segments 19—20, 20—21.

T. orientalis.—Penial setæ with distal extremity flattened and furnished with chevron-shaped ridges. Genital papillæ six or seven pairs between the several segments, immediately following and preceding the seventeenth.

ON THE STRUCTURE AND HOMOLOGIES OF THE SO CALLED PROSTATE GLANDS IN THE OLIGOCHÆTA.

In certain Earthworms the vasa deferentia are unprovided at their external orifice with any glands; this is the case, for example, with Lumbricus, Urochæta, and Microchæta. In other genera glands are present, which either pour their secretion into the terminal region of the vas deferens, or else open on to the exterior independently, but in the immediate neighbourhood of the male generative pores; Perichæta and Pontodrilus are instances of the former condition, while in

Acanthodrilus there are large tubular glands opening close to, but quite independently of, the pores of the male reproductive ducts.

Of these glands there appear to be two different forms. In Perichæta, with the exception of P. Stuarti referred to above (p. 110, footnote), Perionyx, Megascolex, and in many of the Australian Lumbricids lately described by Mr. Fletcher (**11**), these glands, which have received from their position the name of "prostate" glands, are irregularly-shaped, lobate bodies; they communicate with the exterior by means of a thick-walled, muscular duct, which receives at its upper extremity the vasa deferentia. In Acanthodrilus,[1] Pontodrilus, and in some other genera, the prostate glands are somewhat different in form; they consist of a compact tubular gland, which is frequently coiled, but which, like the prostate gland of Perichæta, opens into a thick-walled muscular tube, which in its turn opens on to the exterior. With the upper extremity of the latter, in Pontodrilus, is connected the vas deferens; in some other genera, on the contrary (Acanthodrilus) the gland preserves the same general appearance, and the same histological structure, but is unconnected with the vas deferens.

In Eudrilus the apparent homologues of these glands are very different in their general appearance from those of any other Earthworm, so much so, in fact, that Perrier, their original describer, was inclined to doubt their homology with the prostate glands of other Earthworms. The glands in question are much larger than those of Acanthodrilus, and are straight instead of being coiled. Furthermore, they have a nacreous appearance, which is due to the presence of abun-

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[1] Perrier's figure of the prostate gland in Acanthodrilus ungulatus ('Nouvelles Arch. d. Mus.,' 1872, pl. ii, fig. 18, *pr.*) would seem to indicate that in this species alone the prostates have the racemose characters of those of Perichæta. If, however, Horst ('Notes from the Leyden Museum,' vol. ix, p. 252) be right in assuming that my A. Layardi ('Proc. Zool. Soc.,' 1886) is really the same species, I can state most positively that they are like those of other Acanthodrilus.

dant muscular fibres. I have, however, myself been able to show, in a paper recently communicated to the Zoological Society (6), that these differences only mask a fundamental similarity, and that the minute structure of the glands in Eudrilus closely corresponds to that of the prostate glands in Acanthodrilus. It can be hardly doubted that the "sausage-shaped glands" of Eudrilus are the real homologues of the prostate glands in Acanthodrilus and Pontodrilus.

In Criodrilus (Rosa, Benham) and Allurus (Beddard) the termination of the vas deferens is furnished with a glandular structure, which is not only different in structure from the glands that have been already referred to, but is also unlike in general aspect.

Finally, in Moniligaster (Beddard, 4) the male efferent duct opens into a minute pouch, larger in M. Deshayesi (Perrier 15) and M. Houteni (Horst 14) than in M. Barwelli, which bears a certain resemblance to the prostate of Acanthodrilus, but which, as will be seen hereafter, differs in certain important structural features.

The questions which I shall attempt to answer are: (1) Are these various glandular bodies appended to the vasa deferentia homologous with each other? (2) What relation do they bear to analogous structures in the aquatic Oligochæta?

Moniligaster exhibits a condition of the efferent ducts, which is remarkably different from that of all other Earthworms. In a species (M. Barwelli) recently described by myself (3) the vasa deferentia, as in many Limicolæ, only occupy two segments; there is only a single vas deferens on either side, the internal funnel of which is situated in one segment, and the external aperture on the following segment. The vas deferens opens on to the exterior in common with a glandular structure, which I have called a "prostate" in my account of the anatomy of this worm, and compared with the prostates of other Earthworms.

The structure in question is seen by an examination of transverse sections to contain a wide cavity which opens on to the exterior; the cavity is lined with a layer of large glandular-looking cells; outside these again are abundant muscles followed by a layer of glandular tissue. This latter has a very remarkable structure, which is illustrated in Pl. XII, fig. 11. This figure is a general view of a transverse section of the whole organ, showing the vas deferens (*v. d.*) just at its point of entrance; the external covering is composed of large granular cells, which are separated into groups by partitions. Each cell is prolonged into a fine process, which extends at least as far as the muscular wall; indeed, it is difficult to believe that the cells do not in some way or other reach the lumen of the atrium, and there discharge their glandular secretion.

There is evidently a very close resemblance between these groups of cells and the "prostate" of Rhynchelmis,[1] the prostate of that worm consists of cells with fine long prolongations arranged in groups.

The structure of the organ, in fact, is exactly comparable to that of the atrium in many Limicolæ where the lining epithelium is glandular and of considerable thickness as compared with the surrounding muscular layer.

The atrium of Moniligaster differs from that of Rhynchelmis in the presence of a muscular layer. Vejdovsky does not record the presence of a muscular layer in that worm, nor do his figures show any indication of it. It furthermore differs in the absence of cilia from the cells of the lining epithelium. In Stylaria lacustris[2] a muscular layer is present, and the lining epithelium does not appear to be ciliated. The outer covering of cells is not segregated into groups as in Moniligaster and Rhynchelmis; it consists of a single layer of large glandular cells.

With its single vas deferens occupying only two segments, and opening into an atrium of the character just described, Moniligaster is more like certain Limicolæ than any other Lumbricid.

In my former paper on Moniligaster I was unable to

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[1] Vejdovsky (18), p. 332, pl. xxiv, figs. 1, 3.

[2] Vejdovsky (19), pl. iv, fig. 10.

figure or describe the funnel of the vas deferens; I could only ascertain that it became continuous with the seminal reservoir (erroneously termed "testis"). I have since discovered the funnel by means of transverse and longitudinal sections.

The seminal reservoir appears to perforate the mesentery which divides segment 8 from 9, and to lie in both of these segments (see diagram, Pl. XII, fig. 12). I am inclined to believe that this appearance is produced by a bulging of the mesentery, which is thin and delicate, and that the seminal reservoir really lies in segment 8 attached to the posterior wall of that segment. Its cavity is not divided up by anastomosing trabeculæ as is the case with Lumbricus, &c. The funnel of the vas deferens opens into the interior of the seminal reservoir, and it is important to observe that the funnel is very simple in form as in many Limicolæ, and is not folded and plaited as is usually the case in Earthworms.

There is some discrepancy between my account of the anatomy of Moniligaster Barwelli and M. Perrier's description of M. Deshayesi; this discrepancy is indeed too great to be explained away on the grounds that the species investigated were different.

In a recent paper Dr. Horst has described a third species, M. Houteni; a study of this interesting paper gives me more confidence in restating my own results, which I have every reason now to believe are substantially correct.

Moniligaster, therefore, in respect of its efferent ducts, is nearer to such Limicolæ as Stylaria than any other Earthworm.

Having shown that the male reproductive ducts and the accessory organs of the aquatic Oligochæta are repeated down to the most minute detail in Moniligaster, it remains to be seen how far they are represented in other Earthworms.

Vejdovsky has pointed out in his great work on the anatomy of the Oligochæta (**19**) that the prostate gland of Pontodrilus is probably the homologue of that of Eudrilus. On the other hand, he regards the prostates of Perichæta, Acanthodrilus, Digaster, &c., as equivalent to the prostates ("Cementdrüsen") of the Tubificidæ, and therefore by implication different from the analogous glands in Eudrilus and Pontodrilus, which may possibly represent the atrium of the Tubificidæ. These views are naturally put forward with some little hesitation.

I am disposed partly to agree and partly to disagree with Vejdovsky's conclusions.

I entirely agree with his opinion that the so-called prostates in Eudrilus and Pontodrilus are the homologues of the atrium in the Tubificidæ; I shall, however, bring forward reasons for believing that the prostates in Acanthodrilus, Perichæta, &c., are the homologues of those of Eudrilus, and therefore also of the atrium in the Tubificidæ and other families of the "Limicolæ."

In Eudrilus I have been able to show (6) that the vasa deferentia open into the interior of the large glandular body of the seventeenth segment. The relation therefore of the vasa deferentia to this body is precisely that of the vasa deferentia to the atrium in the aquatic forms. It is true that the vasa deferentia are not connected with the extremity of the supposed atrium as in Moniligaster, Stylaria, &c.; but in the Lumbriculidæ the vasa deferentia also communicate with the atrium about half way down.

The atrium consists of two regions—of a glandular portion and of a muscular tube prolonged into a penis. This differentiation of the atrium has its counterpart in the Tubificidæ, and, moreover, the invaginated penis sheath of the latter is the equivalent of the "bursa copulatrix" of Eudrilus. The atrium in both consists of an epithelial lining and a muscular layer. The epithelial lining is more complicated in Eudrilus than in Tubifex; in Tubifex and apparently in the Limicolous forms generally the lining epithelium of the atrium is a single layer of ciliated cells: this condition, minus the cilia, is retained in Moniligaster. In Eudrilus the lining epithelium of the atrium has the complicated structure which I have already described. There is undoubtedly a close agreement in structure between the glandular cells which compose the greater part of the atrial epithelium in Eudrilus and the cells which cover the atrium in the Lumbriculidæ and in Moniligaster (Pl. XII, fig. 11). Outside this muscular layer, which covers the glandular lining, are faint traces of a peritoneal investment, and it is this which is the homologue of the glandular sheath in Rhynchelmis, Moniligaster, &c. The explanation of the difference in the structure of the atrial epithelium is, as it appears to me, quite another one.

It has been conclusively proved by Vejdovsky that the atrium in the Tubificidæ is formed by an ectodermic involution just as are the spermathecæ and the "vesicle" of the nephridia, and as a consequence it retains the structure of the integumental layers. The ciliation of the lining epithelium is particularly interesting in this connection, because it often happens that ectodermic involutions, owing to the protection which they afford, retain the ciliated condition which is lost on the general body surface. Moreover, the cells in the distal glandular part of the atrium in the adult have more completely retained the characters of the epidermis than in the proximal region, where it has undergone secondary modifications in connection with the formation of the penis.

In Eudrilus the male reproductive pores are intraclitelline. It is a fair assumption to suppose that the atrium is invaginated from the ectoderm, and it will therefore retain to a certain extent the structure of the body wall as it does in Tubifex. The ectodermic cells in the young embryo, at the point where the atrium is invaginated, have the potential capacity of developing into the complicated clitellar epidermis; it is therefore not surprising to find that the invaginated cells also retain this capacity, and ultimately form an epithelium nearly identical in structure with the clitellum. The objection that those cells which are nearest to the point of invagination are most unlike the clitellar epidermis is to be met by reference to Tubifex. The absence of cilia may be reasonably accounted for on the supposition that Eudrilus is farther removed from the ancestral ciliated condition than Tubifex.

In Acanthodrilus, Pontodrilus, and Typhæus the muscular layer of the atrium has been lost, and only a delicate peritoneal layer[1] remains; otherwise the structure of the atrium is the same; it is therefore probable that in all these forms (even Pontodrilus, which is now post-clitelline) the atria have been invaginated from the clitellar area. On the other hand, in Moniligaster the simple epithelium of the atrium may perhaps indicate that it has not been formed as an ingrowth from the clitellar area. This supposition is supported by the forward position of the atria in this worm.

Professor Bourne has, however, lately (8, p. 662) described a species of Moniligaster where a clitellum is present in the neighbourhood of the male pores.

I therefore make the above suggestion, which indicates a possible confirmation of Perrier's classification of Earthworms, with considerable hesitation.

In Pontodrilus the atria have acquired the character of an appendage of the vas deferens, and the penis is absent.

In Typhæus the independence of the atria and the vasa deferentia is more marked. The two organs appear to open on to the exterior of the body independently, but in reality they unite just below the epidermis.

In Acanthodrilus the vasa deferentia open on to the exterior, quite independently of either of the two tubular glands of the seventeenth and nineteenth segments.

In my paper on Acanthodrilus (1) I have wrongly stated that the two vasa deferentia of each side communicate with the two tubular glands. I have since found that in A. multiporus and A. dissimilis this is not the case. The vasa deferentia open on to the exterior on the eighteenth segment, close to the ventral pair of setæ; they open by a single pore, and only unite just before the external pore. It is probable, therefore, that in Acanthodrilus generally there

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[1] In Trigaster Benham has made the interesting observation ('Quart. Journ. Micr. Sci.,' vol. xxvii) that the muscular layer of the atria is partially retained.

is only a single male pore situated on the eighteenth segment (see above, p. 102).

Ocnerodrilus (Eisen **12**) offers an interesting parallel. In this Annelid there is a saccular body opening in common with the vasa deferentia, which is probably, as Vejdovsky has suggested, the atrium.

There seems, indeed, to be little doubt that the so-called prostates in these types are (i) homologous with each other, and (ii) are homologous with the atria of the aquatic forms. A gradual series of transitions unites Eudrilus, which is the least modified, with Acanthodrilus, which stands perhaps at the other extreme. It is possible that the division of the atrium in Eudrilus (Beddard **6**) bears some relation to the double atria of Acanthodrilus, but I have not yet thoroughly investigated this point. The term "prostate" must therefore be no longer applied to these glands.

The racemose glands of Perichæta, &c., now remain for consideration, and the question which must be answered is: Are these glands the homologues of the prostates of the Tubificidæ, or do they correspond to the atria of Eudrilus and Acanthodrilus?

The structure of these glands is as follows:—They consist of a series of branching ducts, lined with a single non-ciliated cubical epithelium; the ducts appear to end blindly, but groups of glandular cells are attached to them here and there, and doubtless void their secretion into the ducts. The ducts unite into a main duct, which opens in common with the vas deferens into a thick-walled muscular tube, which, at least in Perichæta Houlleti, can be evaginated, and probably serves as a penis. The glandular cells are exactly similar in their structure to the cells of the prostate in the Tubificidæ; they also resemble the glandular cells of the atrium in Pontodrilus (cf. Pl. XIII, figs. 12, 13). At first sight, therefore, three hypotheses seem to be possible: either the whole structure corresponds to the atrium of Acanthodrilus, differing only in the branching of the cavity and in the segregation into groups of the glandular cells, or the ducts alone are collectively the homologues of the glandular region of the atrium in Acanthodrilus, and the groups of glandular cells are the homologues either of the Cementdrüsen of Tubifex or of the glandular covering of the atrium in Rhynchelmis and Moniligaster. The crucial fact, however, which to my mind settles the latter homology, is the presence of a delicate peritoneal layer surrounding the whole organ. In Moniligaster and in Rhynchelmis, &c., there is no peritoneal layer surrounding the prostates, for the very sufficient reason that the prostates are themselves the modified peritoneal cells. All the structures, therefore, which lie within the peritoneal layer must belong to the atrium; the so-called prostate of Perichæta is therefore not the homologue of the glandular investment of the atrium of Rhynchelmis and Moniligaster.

There are some difficulties in the way of a comparison between the prostate of Tubifex and that of Perichæta. It is true that there is a very considerable superficial similarity. The origin of the prostate in the Tubificidæ from the epithelium of the atrium has been followed by both Vejdovsky and Eisen; these facts therefore are in favour of the comparison. On the other hand, it seems on a priori grounds likely that the prostate of Perichæta is the homologue of the atrium in Acanthodrilus; in this case, as already pointed out, the glandular cells must correspond in both genera; in the Tubificidæ the atrium is lined by a single layer of cells, some of which become modified into the prostate gland; the superadded glandular layer of the atrium is altogether wanting. I should be inclined, therefore, for the present to regard the prostate of Tubifex as not strictly homologous with the so-called prostate of Perichæta.

Although the structure of the "prostate gland" in the majority of Perichetæ is like that of P. Houlleti described above, and presents therefore considerable resemblances to the prostate glands of the Tubificidæ, this is not always the case. In a species (P. Newcombei) which I have recently described from Australia, and which is probably identical with one of those described by Fletcher (11), the prostate glands (Pl. XIII, fig. 15) have a tubular form like those of Acanthodrilus; this fact is also noted by Fletcher. I find, however, that these glands are really branched like those of other Perichetæ (Pl. XIII, fig. 13), but there is only a faint indication of the division of the gland into lobules. The structure of the gland in this species is therefore intermediate between the ordinary Perichetæ and Acanthodrilus, &c. It has been said that the structure of the atrium in Acanthodrilus is identical with that of the corresponding organ in Perichæta, allowing only for the branched character of the supposed atrium in Perichæta. In Perichæta, however, the lining epithelium (Pl. XIII, fig. 13) is distinctly columnar and not glandular; it is very sharply marked off from the surrounding glandular layers. In Acanthodrilus (Pl. XIII, fig. 14) and Deinodrilus (Pl. XIII, fig. 16) the lining epithelium is loaded with granules, and is on that account rather difficult to distinguish from the glandular layers surrounding it; in any case, this difference does not appear to me to be one of importance; but if it were then Pontodrilus could hardly be referred to either category. The layers of cells which form the atrium (Pl. XIII, fig. 12) are like those of Perichæta in the obvious difference between the innermost layer of cells and those which surround them; the cavity of the atrium is, however, unbranched like that of Acanthodrilus. This series of facts leads me to believe that the so-called prostates of Perichæta are equivalent to the atria of Acanthodrilus and Pontodrilus, &c.

In Criodrilus Rosa (17) has recorded the presence of a gland surrounding the external orifice of the vas deferens. This he has termed the atrium. The investigations of Benham have shown that this supposed atrium is nothing more than a group of cells continuous with the clitellum. I have found the same thing in Allurus.

The vas deferens passes through the glandular body and opens on to the exterior; it undergoes no changes in its character (in Allurus), and the terminal section is not in any way widened out to form a chamber which might be compared with an atrium. The term prostate, in the sense in which it has been used in the foregoing pages, is not applicable to the mass of glandular cells which surround the end of the vas deferens in Allurus; the structure in question is more rightly to be compared to such a group of glandular cells as that which surrounds the termination of the vas deferens in the Enchytræidæ (Vejdovsky **19**).

SUMMARY.

The most important facts described in the present paper are:

(1) The independence of the vasa deferentia and atria in Acanthodrilus (Pl. XIII, fig. 12); the two vasa deferentia of each side unite just before their opening on the eighteenth segment. The atria (= "prostates") open separately upon the seventeenth and nineteenth segments.

(2) The independence of the single vas deferens and its atrium in Typhæus; they open near together on the same segment—the seventeenth (Pl. XII, fig. 1).

(3) The occurrence of six pairs of setæ in each (setigerous) somite of Deinodrilus (Pl. XIII, fig. 9).

(4) The completely double dorsal blood-vessel of Acanthodrilus annectens and of Deinodrilus Benhami.

(5) The enclosure of each half of the dorsal vessel of Deinodrilus in a separate cœlomic space (Pl. XIII, figs. 6, 7).

(6) The presence in Moniligaster Barwelli of an atrium consisting of a thick glandular covering of peritoneum of a layer of muscular fibres, and finally, of a single layer of columnar epithelium (Pl. XII, fig. 11). The atrium is similar in structure to that of Rhynchelmis.

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EXPLANATION OF PLATES XII, XIII,

Illustrating Mr. Frank E. Beddard's Paper "On the Structure of Three New Species of Earthworms, with Remarks on Certain Points in the Morphology of the Oligochæta."

PLATE XII.

Figs. 1—9.—Typhæus Gammii.

Fig. 1. Male reproductive organs. *T.* Testis. *M.* Septum. *a.* Part of seminal vesicle. *f.* Funnel of vas deferens. *v. d.* Vas deferens. *s.* Setæ of ventral pair. *gl.* Glandular part of atrium. *s'.* Sac containing penial setæ. *m.* Muscular part of atrium.

Fig. 2. Transverse section through a portion of one of the intestinal glands.

Fig. 3. Segments in the immediate neighbourhood of the male reproductive pores, to show copulatory papillæ.

Fig. 4. Supra-œsophageal ganglia. *v.* Visceral nerves. *c.* Circum-œsophageal commissure.

Fig. 5. Section through junction of atrium and setæ sac. *s.* Penial seta.

Fig. 6. Principal vascular trunks. *d.* Dorsal vessel. *v.* Ventral. *si.* Supra-intestinal. *e.* Epidermis.

Fig. 7. Anterior segments, to illustrate the number of annuli in each segment. *cp.* Orifices of spermathecæ.

Fig. 8. Œsophagus in the region of calciferous glands (*ca.*).

Fig. 9. Dissection of the thirteenth and fourteenth segments. *v. d.* Vas deferens. *ov.* Ovary. *od.* Oviduct.

Figs. 10—12.—Moniligaster Barwelli.

Fig. 10. Section through a body in the tenth segment, which is probably the oviduct.

Fig. 11. Transverse section through atrium. *v. d.* Vas deferens. *pr.* Glandular peritoneal cells. *bl.* Blood-vessels.

Fig. 12. Diagrammatic longitudinal section through anterior region of body. *s.o.* Supra-œsophageal ganglion. *s.* Salivary glands. *sp.* Septum. *at.* Atrial pore. *v. s.* Seminal vesicle. *od.* Oviduct. *cp.* Spermatheca.

Fig. 13.—Acanthodrilus annectens. Dissection of genital segments. *t.* Testes. *ov.* Ovary. *od.* Oviduct. *f.* Funnel of vas deferens.

PLATE XIII.

Fig. 1.—Typhæus Gammii. Penial seta.

Fig. 2.—Typhæus orientalis. Penial seta.

Figs. 3—10.—Deinodrilus Benhami.

Fig. 3. Ventral view of genital segments. *cl.* Clitellum.

Fig. 4. First three segments of the body.

Fig. 5. Spermatheca.

Fig. 6. Transverse section through dorsal blood-vessels. *m.* Muscular layer of blood-vessel. p''. Peritoneal covering. p'. Peritoneal lining of perihæmal space. *p.* Peritoneal covering of perihæmal space. *E.* Intestinal epithelium. *bl.* Blood-space. *t.* Peritoneal cells covering intestine.

Fig. 7. Longitudinal section of the same, lettering as above.

Fig. 8. Typhlosole in transverse section.

Fig. 9. Diagrammatic section of body, to illustrate arrangement of setæ.

Fig. 10. Transverse section through body wall.

Figs. 11—12.—Acanthodrilus annectens.

Fig. 11. Spermatheca.

Fig. 12. Transverse section through pore of vasa deferentia and apertures of atria. *v. d.* Vas deferens. *p.* Atrium of seventeenth segment. ♂ aperture of vas deferens. *m.* Intersegmental septa. *at.* Atrial pore of nineteenth segment.

Fig. 13.—Transverse section through atrium of Perichæta Newcombei. *a.* Peritoneal covering. *b.* Glandular cells. *c.* Lining epithelium.

Fig. 14.—Transverse section through atrium of Acanthodrilus; lettering as above.

Fig. 15.—Atrium of Perichæta Newcombei, drawn with camera lucida. *vd.* Vas deferens.

Fig. 16.—Longitudinal section of part of atrium of Deinodrilus Benhami; lettering as in Fig. 13.

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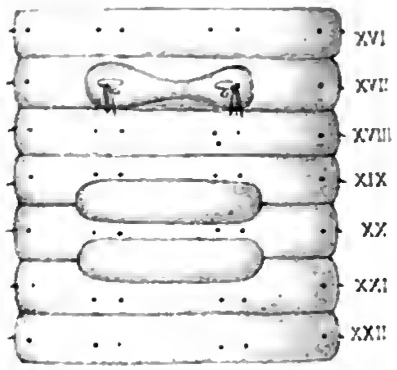

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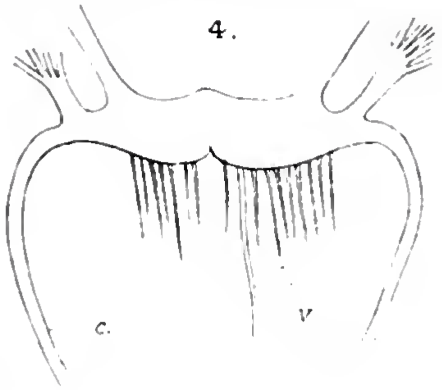

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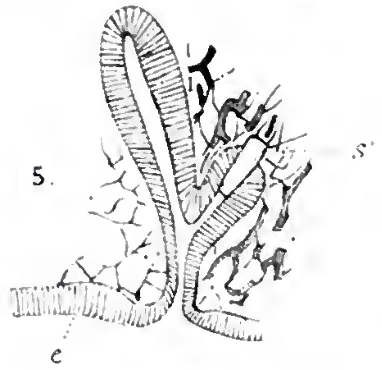

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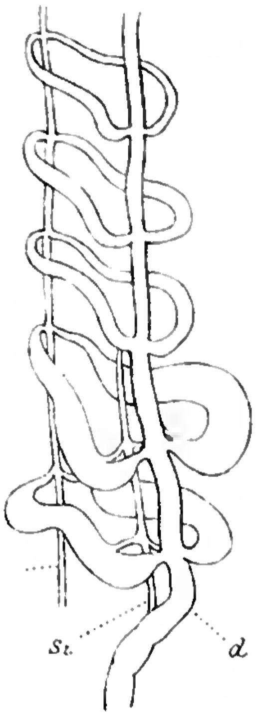

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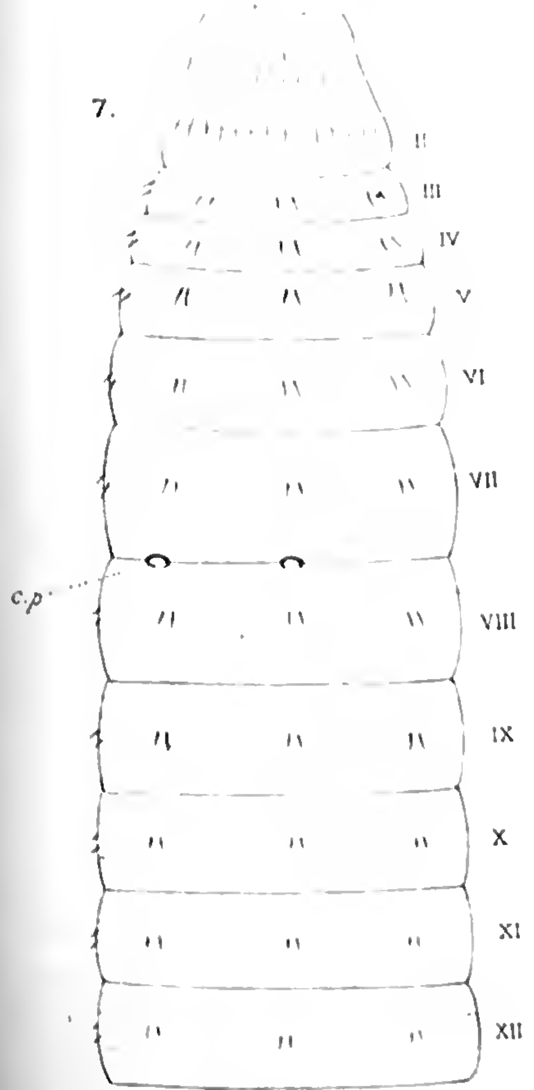

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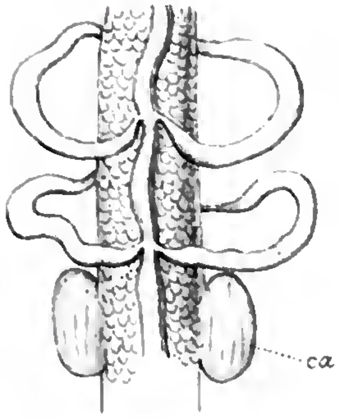

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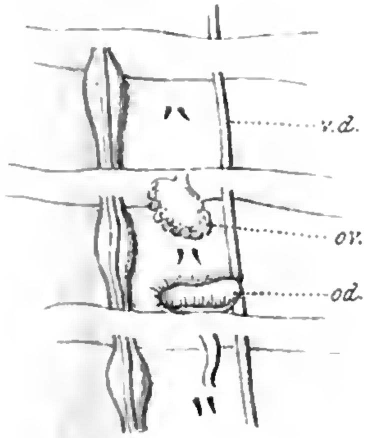

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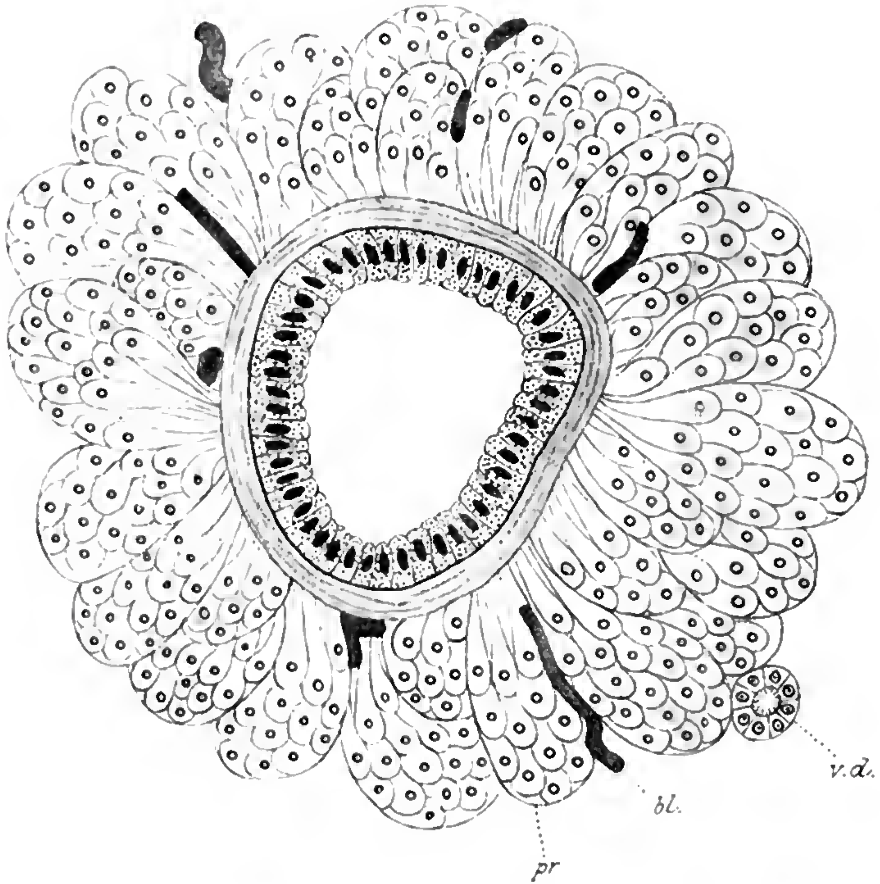

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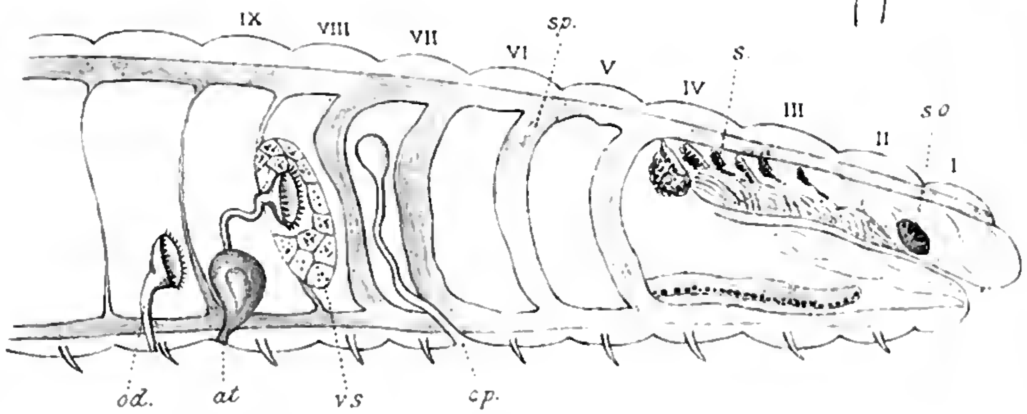

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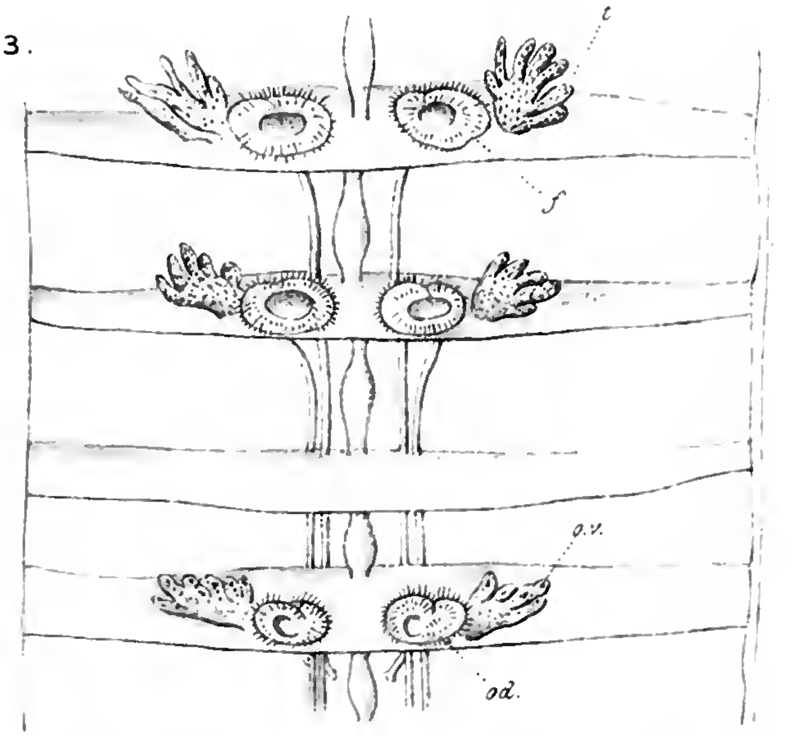

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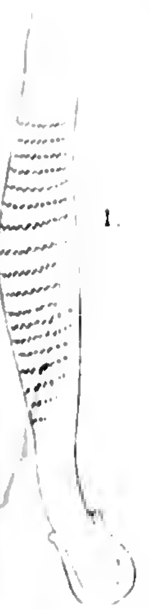

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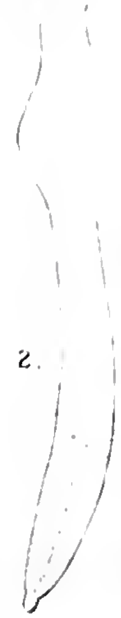

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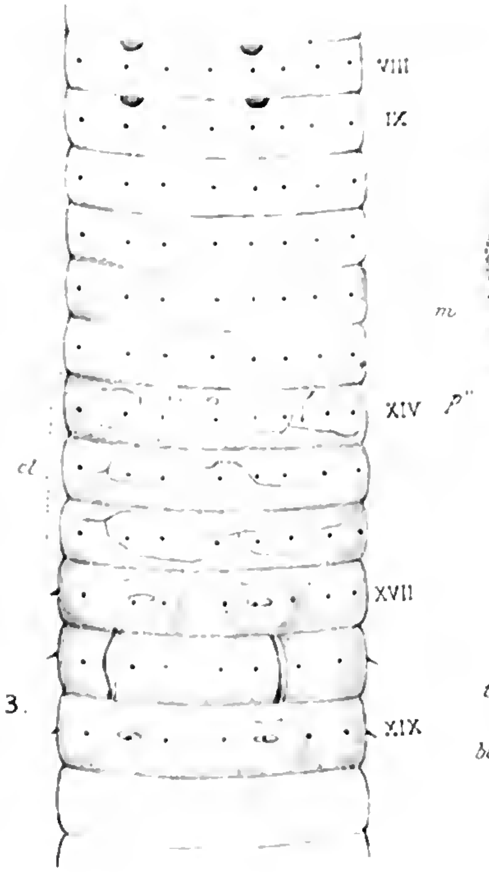

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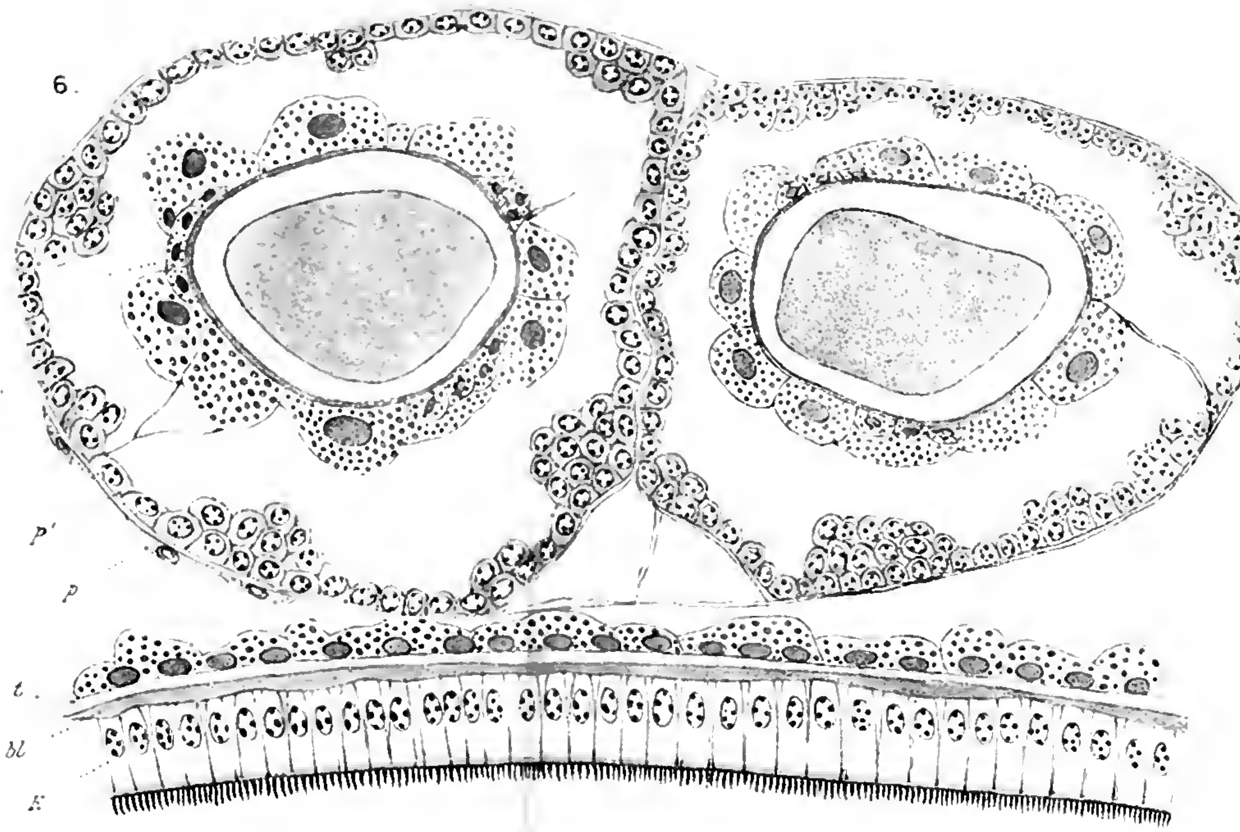

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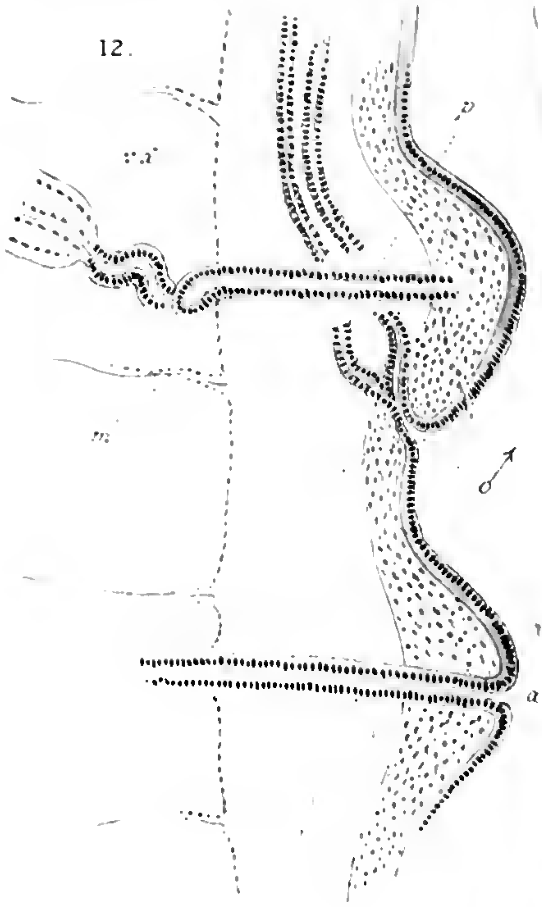

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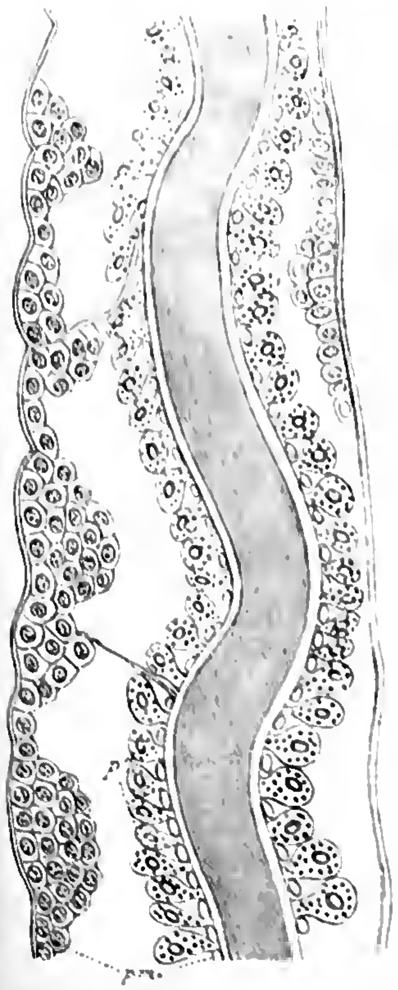

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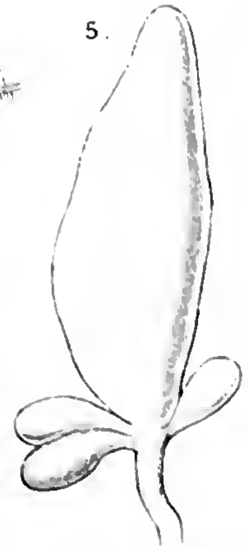

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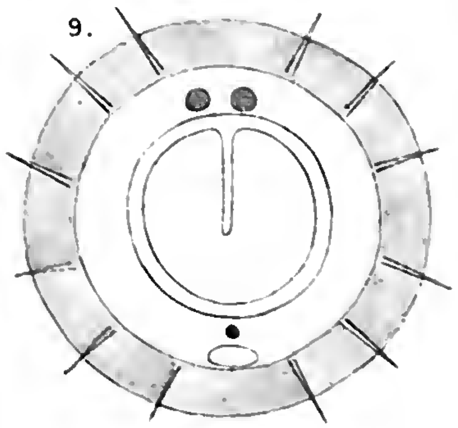

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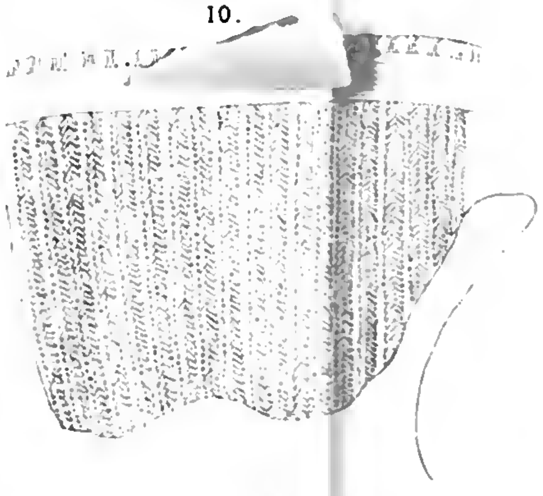

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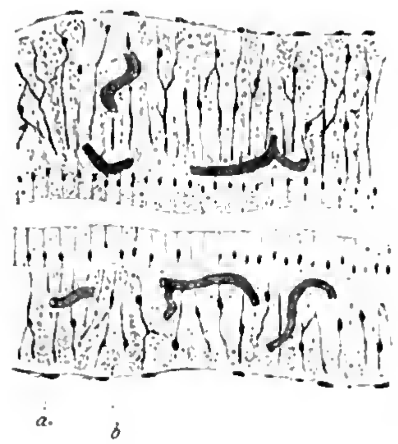

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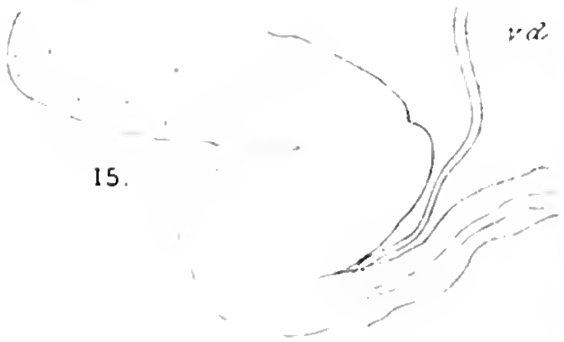

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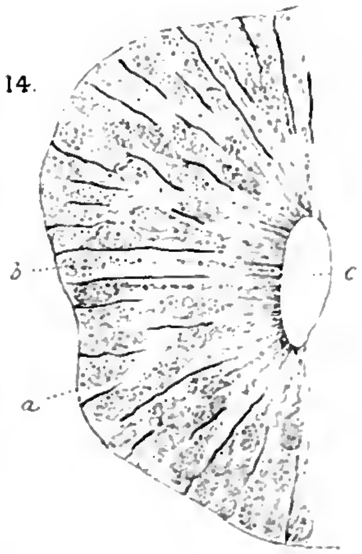

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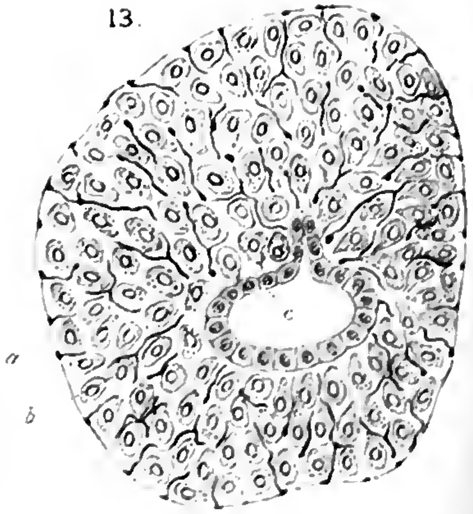

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Development of the Fat-bodies in Rana temporaria. A Contribution to the History of the Pronephros.

By

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With Plate XIV.

It has generally been held, since the researches of von Wittich, that the fat-bodies, or corpora adiposa, in the Frog and allied Amphibians, are derived from the genital organs by a process of fatty degeneration in the anterior end of the primitive genital ridge.

Von Wittich himself says[1] "they (the fat-bodies) have not at any time any connection with the Wolffian bodies, nor with the kidneys or their ducts." And again, "the genital organs become constricted into an anterior and a posterior part, of which the anterior becomes the fat-body, and the posterior the genital organ."

This investigation, conducted in the biological laboratories of Owens College, was begun with the intention of ascertaining if these views of von Wittich were correct. But its progress showed that the mode of development of the fat-bodies is very different from what von Wittich thought, and that the changes which take place are of a very interesting nature.

On dissecting a tailed Frog, as represented in fig. 1, the fat-bodies were seen already beginning to take on the lobose form

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[1] 'Beitrage zur morphologischen und histologischen Entwickelung der Harn und Geschlechts Werkzeuge der nackten Amphibien," 'Zeits. für wiss. Zool.,' 4te Band, 1853, pp. 148, 149.

which characterises them later on, and having in this case a peculiar resemblance to the fingers of a hand, as represented in the right half of fig. 2. Thinking that the light-coloured bodies from which they sprang were the genital organs, these were removed with the surrounding parts, and cut horizontally in successive sections. It was then found that what had been taken macroscopically for genital organs (the real genital organs not appearing so plainly as in fig. 1) showed microscopically most typical kidney structure, whilst at the same time it was quite continuous with the fat-body at the anterior end.

Two questions naturally arise: (1) How come the fat-bodies to be in relation with the anterior end of the kidneys? (2) How does the transition from this condition to that found in the adult take place? These questions I propose to answer in the following account.

Up to the age with which we are concerned, the generative cells are found in the condition of primordial ova, as described by Balfour;[1] hence there is no differentiation into ovary and testis. I shall therefore uniformly use the neutral term "genital organ."

The method adopted was to begin with very young tadpoles, and cut series of sections at various stages and in various planes, with the following results.

In a tadpole 8 mm. long, that is, soon after the first appearance of the external gills, the three primitive openings of the pronephros into the body-cavity can be seen. The tubules forming the pronephros are actually of larger diameter than they are somewhat later. One of them is represented in fig. 3, in which it is seen that the cells lining the tubules are cubical or columnar, granular at the part nearest the lumen, and showing a distinct radial striation peripherally. The nucleus is central, and stains readily, as does also the nucleolus. The genital organ at this stage is situated nearer the median line than the pronephros, and anterior to it, and is well defined both anteriorly and posteriorly.

The young tadpole at the stage we are considering has still a

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[1] 'Comparative Embryology,' vol. ii, p. 747.

plentiful supply of food-yolk, and is consequently independent of nutrition obtained from without. But now, as it grows, the absorption of the food-yolk proceeds more rapidly, while at the same time certain changes are observed, notably the gradual atrophy and subsequent disappearance of the external gills, while the recently acquired internal gills take on more work.

If at this stage the pronephros be examined, it will be seen that the tubules have a narrower diameter than those of the younger tadpole, while the cells are not so clearly defined. By this time the number of funnel-like openings into the body-cavity has increased from three to five, and a new and important structure has made its appearance, the mesonephros, developed, as Sedgwick has shown,[1] in the mesoblast independently of the peritoneal epithelium.

The meso- and meta-nephros are not distinct from one another in the tadpole; they together form the kidney as found in the adult, and it is in this sense that the word kidney will be used.

The mesonephric tubules extend gradually from behind forwards till they come in contact with the pronephros. The whole nephros then acquires a distinct capsule, becomes separated from the muscular substance of the lateral mass, and lies freely in the abdominal cavity on the ventral aspect of the vertebral column, the peritoneum passing over it. Between the two kidneys is the aorta (fig. 5). The genital organs, which arise as two hollow ridges, also gradually separate from the body wall, lying internal and ventral to the kidneys (fig. 5), and are still perfectly well defined anteriorly, the proper genital substance extending quite to the anterior end.

Concurrently with these changes of conformation, the structure of the pronephros has been undergoing modification of the nature of a fatty degeneration. At the time that the hind limbs are just making their appearance, the degeneration has gone on to the extent represented in fig. 4.

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[1] "On the Early Development of the Anterior Part of the Wolffian Duct and Body in the Chick, together with Some Remarks on the Excretory System of the Vertebrata," 'Quart. Journ. Micr. Sci.,' vol. xxi, N. S., 1881, p. 449.

The way in which this conversion of kidney parenchyma into fat takes place is a true fatty degeneration, and not simply a fatty infiltration, though the latter occurs in the first stage. The change is seen best in the cells lining the glomeruli and renal tubules. The clearly defined margins of the cells become hazy, and the nuclei less distinct; fatty droplets appear at various parts of the cell and run together. The cells do not, however, swell up as the fatty matter invades them, but their protoplasm becomes replaced by it. At a later stage the contents of the cell consist only of fatty granules and granular detritus.

For a while the outlines of the convoluted tubules can still be made out, as in fig. 6, the line of distinction between normal and degenerated kidney being well marked. But soon all trace of structure disappears, and there remains only a uniformly granular-looking mass, as in fig. 2. This is the fat-body, or corpus adiposum.

We have thus answered the first question that we proposed, "How come the fat-bodies to be in relation with the anterior end of the kidneys?" There further remains to be considered the question, "How does the transition from this condition to that found in the adult take place?"

When the hind limbs of the tadpole have appeared they develop fairly rapidly, the fore limbs sprouting out somewhat later. The condition of the "tailed Frog" is now attained. While this is going on a change takes place in the urino-genital organs, which, as regards the time at which it occurs, varies somewhat in different tadpoles, but usually begins during the period in which the tail is commencing to atrophy, and is for the most part completed by the time the tail is quite absorbed.

This change is as follows: the anterior end of the nephros grows ventrally, and becomes secondarily attached to the anterior end of the genital organ, ovary or testis, as the case may be. Fig. 7 shows the urino-genital organs during this intermediate stage of transition, the fat-body (*f.*) being directly continuous both with the kidney (*k.*) and with the genital organ (*g.*).

This occurs at about the time that the mesonephric tubules are growing out towards the genital organ, forming the future vasa efferentia in the case of the male. Thus in some sections the condition of this double outgrowth from the excretory to the genital organs can be seen, the three parts of the nephros, pro-, meso-, and meta- being quite continuous.

Ultimately the attachment of the fat-body to the kidney gives way, and the former remains attached to the anterior end of the genital organ, as it is in the adult (figs. 8 and 9). We thus see that the fat-body is not the anterior end of the genital organ, which has undergone fatty degeneration, as was thought by von Wittich, but that its attachment to the genital organ is secondary.

The fatty degeneration is always complete before the attachment to the genital organ takes place; almost any tailed Frog that has not very long had its four limbs showing the fat-body attached to the anterior end of the kidney. That it is, in reality, fat-body is shown by its macroscopic and microscopic characters, and by its staining with osmic acid. The part marked (*f.*) in fig. 7 has exactly the same structure and appearance as that similarly marked in fig. 8, the two specimens having been stained and cut at the same time.

Having thus decided that the fat-bodies are derived not from the genital organs but from excretory structures, we have to consider what part of the nephros it is to which they owe their origin. It can only be pro-, meso-, or meta-nephros, or their ducts; the ducts can be at once put aside, because their destination has been clearly and definitely made out. The meso- and meta-nephros are also known to form together the permanent kidney, as found in the adult.

There remains, therefore, only the pronephros, which, in the Amphibians at least, has hitherto received but little attention, though Sedgwick[1] mentions that it undergoes atrophy in the young Frog. "Atrophy," however, implies diminution in size, or even total disappearance; the pronephros of the tadpole, on the contrary, not only persists but actually gets larger (in

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[1] Op. cit., p. 445.

its modified form) as the Frog grows. Now, we saw that at an early stage the pronephros undergoes a fatty degeneration; that the degenerated part remains for a time continuous with the rest of the kidney (fig. 6), and then becomes secondarily attached to the genital organ. Hence the fat-bodies represent the persistent pronephros, profoundly modified both in structure and in function.

If it be objected that it is a priori improbable that the fat-bodies should consist of the anterior part of the nephros detached and fastened on secondarily to the genital organ, it will be sufficient to recall the fact that the vasa efferentia are formed by a quite parallel growing out of kidney structure—the mesonephric tubules; the only difference being that the process in the case of the fat-body goes a step farther, since the primary connection with the kidney is lost, while the vasa efferentia remain connected with both kidney and testis.

Again, the question may be asked, "Why should only a part of the kidney structure undergo fatty degeneration—why should not the meso- and meta-nephros share in the change?" The answer would be even more difficult to find if, on the supposition that von Wittich was right, such a question were asked concerning the genital organs, for they are of equal value in all their parts, and when the metamorphosis occurs no portion of them has had any reproductive activity. But in the case of the pronephros it is different. It is true that the nature and origin of the pronephros are still matters of discussion, but it is at least evident that the pronephros is in many respects different from the mesonephros; that the former, in the case of the Frog and of all animals with a larval stage, has a period of activity before the mesonephros appears at all, and in most cases disappears as the latter begins to take on active functions. On the other hand, in Vertebrates possessing no larval stage, the existence of the pronephros is only dimly shadowed forth by rudimentary traces, the meso- and meta-nephros performing all the excretory functions from the first.

The answer then to the question, "Why this change should occur resulting in the formation of the fat-body," seems to be this—that with the close of larval life the pronephros is no longer needed, and in harmony with the pathological law that atrophy follows disuse, it degenerates to the condition of fat-body. Doubtless, however, this law is here so far modified that the fat-body still serves some useful purpose in the organism, though what that purpose is is not at all clear. It is in all probability an example of "change of function," the later function being in some way nutritive.

As to the distribution of fat-bodies—they are unknown outside the Amphibian group. According to Stannius, Hoffmann, Wiedersheim, and others, they are present in all Amphibians. We have very little knowledge of their function beyond that they are concerned in all probability with nutrition, serving as a reserve stock at certain times of the year. They are differently placed in the several groups in which they occur, and it is by no means certain whether they are homologous structures in all cases.

The fate of the pronephros in the Frog, as above-described, throws some light on the condition that obtains in other groups of Vertebrates.

It was stated by Balfour[1] that "the pronephros atrophies more or less completely in most types, though it probably persists for life in the Teleostei and Ganoids."

In a later paper,[2] however, after working over the condition of the kidneys in the sturgeon and in certain Teleostei, he stated that "the whole of the apparent kidney in front of the ureter, including the whole of the so-called head-kidney, is simply a great mass of lymphatic tissue, and does not contain a single uriniferous tubule or Malpighian body," from which he concluded that both in Ganoids and in Teleostei the organ usually held to be pronephros is actually nothing of the kind. He therefore considered that Rosenberg[3] was mistaken in

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[1] 'Comparative Embryology,' vol. ii, p. 729.

[2] "On the Nature of the Organ in Adult Teleosteans and Ganoids, which is usually regarded as the Pronephros or Head Kidney," 'Quart. Journ. Micr. Sci.,' vol. xxii, N. S., 1882.

[3] 'Untersuchungen über die Entwicklung der Teleostierniere,' Dorpat, 1867.

thinking that he had traced in the pike the larval organ into the adult part of the kidney called by Hyrtl the pronephros; and his final conclusion was "that the pronephros, though found in the larvæ or embryos of almost all the Ichthyopsida, except the Elasmobranchii, is always a purely larval organ, which never constitutes an active part of the excretory system in the adult state." But Balfour did not apparently regard it as possible that the pronephros might continue in the Ichthyopsida in a modified condition, but thought that if it did not persist with at least its original structure, if not its original function, it must have disappeared altogether. He was, however, led to this conclusion by the study, not of their development, but of their adult structure.

But it seems to me, from a consideration of the state of things in the tadpole and young Frog as above described, that it is not at all necessary that the pronephros, if it persist, should retain its original structure any more than its original function; that it is quite possible that Rosenberg's observations were correct, since the only argument adduced against them is this alteration of structure, and that there is nothing in Balfour's observations on the Ganoids and Teleosteans to contradict them. The fate of the pronephros in Teleosteans and Ganoids is, from this standpoint, closely analogous to that in the tadpole, except that in the latter it undergoes yet further modification in becoming quite separated from the true kidney and attached permanently to the genital organ.

The fact that the pronephros does persist in a modified form seems to me in nowise to detract from but rather to add to the probability of Gegenbauer's views being correct, namely, that the pronephros is the primitive excretory organ of the Chordata, and that its substitute in existing Vertebrata, the mesonephros, is phylogenetically a more recent organ.

I may sum up my conclusions as follows:

I. The fat-bodies in the Frog, and hence presumably in allied Amphibians, are formed by a fatty degeneration, not of the anterior end of the genital organs, but of original kidney structure.

II. The part of the kidney which undergoes this conversion into fat-body is the pronephros or head-kidney.

III. It seems very probable from analogy, and from the researches of Rosenberg, that the structure in front of the true kidney in Ganoids and Teleostei, described by Balfour as lymphatic tissue, is the persistent but structurally and functionally modified pronephros.

IV. The fact that a part of the kidney undergoes such a remarkable change, the rest remaining normal and functional, is an additional argument in support of the view that the pronephros has a different phylogenetic history from the mesonephros, and that it is more ancestral.

It only remains for me to perform the pleasant duty of expressing my warm thanks to Professor A. Milnes Marshall for the uniform and stimulating kindness with which he has helped me in this short research by suggestions and criticisms; he has been good enough to go over my specimens with me, and to discuss with me my results.

I desire also to express my obligations to my friend Dr. G. Herbert Fowler for much valuable and practical assistance.

My thanks are further due to Professor Stirling, under whose direction the work has been done.

DESCRIPTION OF PLATE XIV,

Illustrating Mr. A. E. Giles's paper on "The Development of the Fat-Bodies in Rana temporaria."

The letters have the same significance in all the figures. *b.* Muscles of body wall on the ventral aspect of the vertebral column. *f.* Fat-body. *g.* Genital organ (sex undifferentiated). *k.* Kidney. *n.* Notochord.

Fig. 1.—Tailed Frog, dissected so as to expose the urinogenital organs. The kidneys are seen lying against the vertebral column, and continuous anteriorly with the fat-bodies. Anterior and internal to the kidneys are the genital organs. × 4.

Fig. 2.—Anterior end of the urinogenital organs of the tailed Frog shown in Fig. 1, enlarged. The right half of the figure shows the surface view, the left half shows the appearance in horizontal section. × 50.

Fig. 3.—Normal pronephric tubule, from a tadpole still possessing external gills. × 350.

Fig. 4.—Pronephric tubules showing fatty degeneration, from a tadpole whose hind limbs were just appearing. × 350.

Fig. 5.—Transverse section through the lumbar region of a tailed Frog, showing the mode of development of the genital organs and their relation to the excretory organs at this stage. × 50.

Fig. 6.—Sagittal section through the lumbar region of a tadpole that had recently acquired its fore-limbs, showing the anterior end of the nephros partly degenerated. × 60.

Fig. 7.—Sagittal section through the lumbar region of a tailed Frog whose tail had begun to be absorbed, showing the fat-body connected with both kidney and genital organ. × 60.

Fig. 8.—Sagittal section through the lumbar region of a young Frog that had just lost its tail. × 60.

Fig. 9.—A young Frog at the same stage as the preceding, dissected so as to expose the urinogenital organs, which present the same condition as in the adult. × 4.

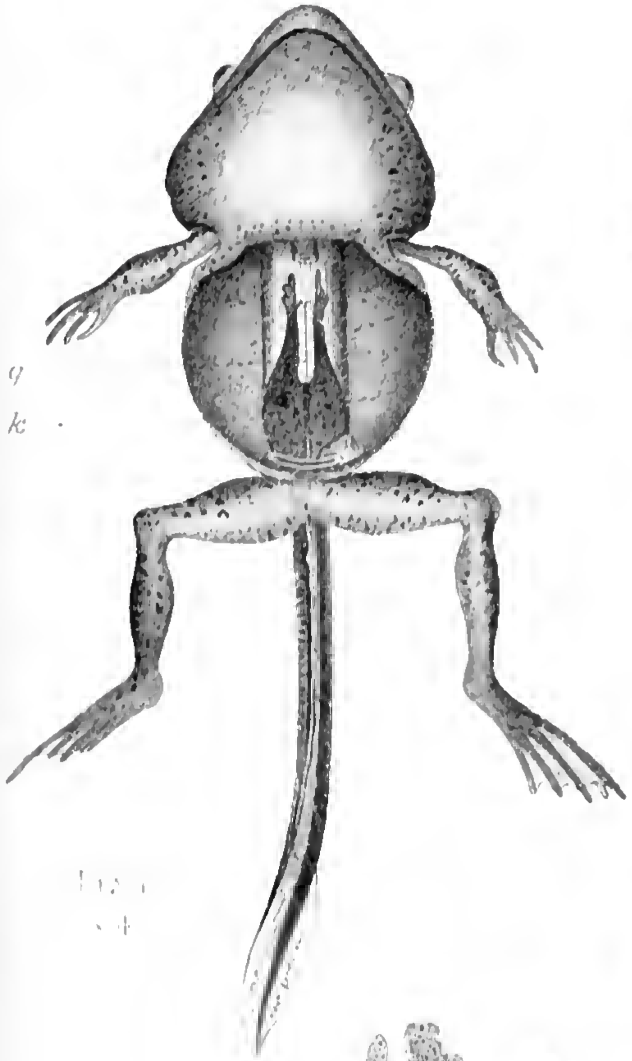


Fig. 1
×4

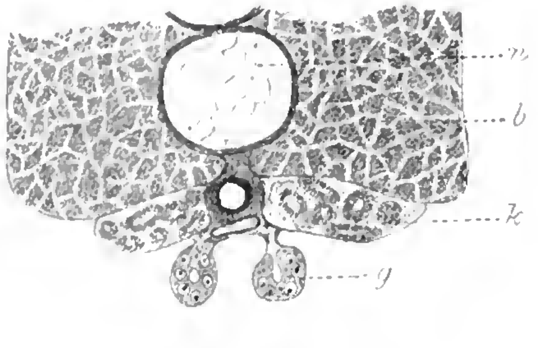


Fig. 5
×50

Fig. 4
×350

Fig. 2
×50

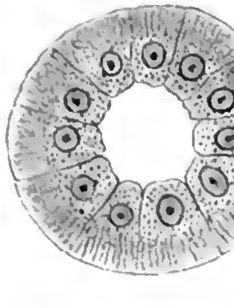


Fig. 3
×350

A. E. Giles del.

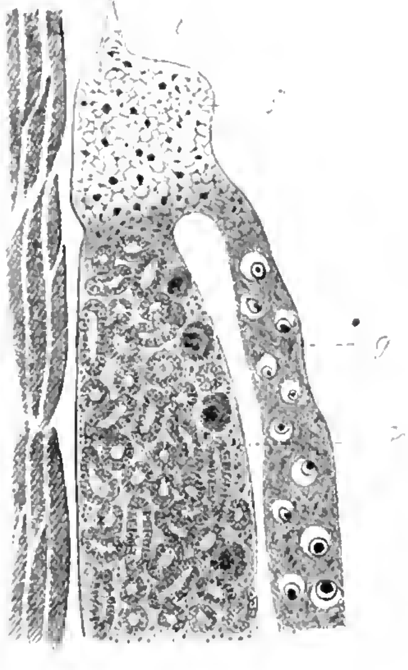


Fig. 7
×60

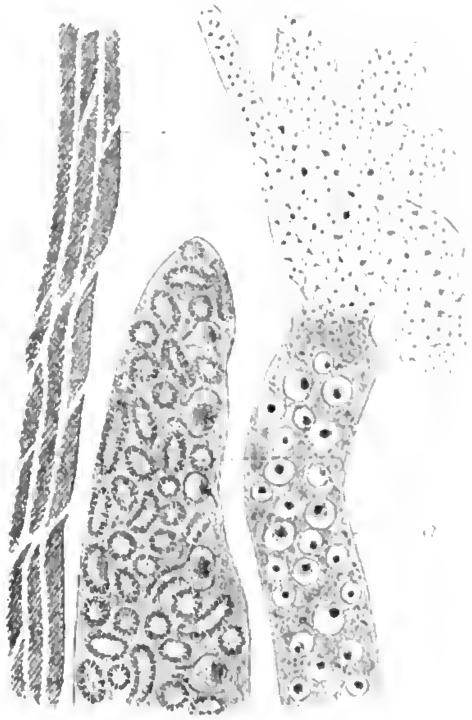


Fig. 8
×60

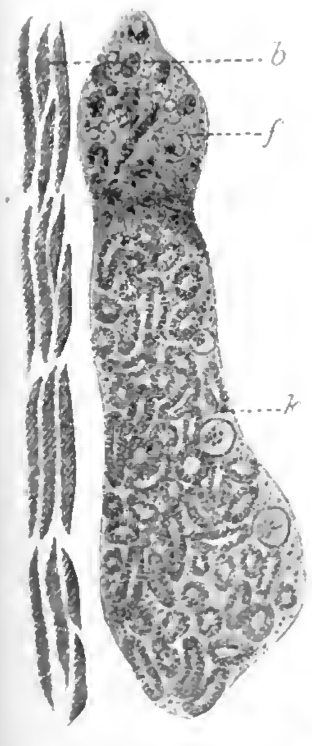
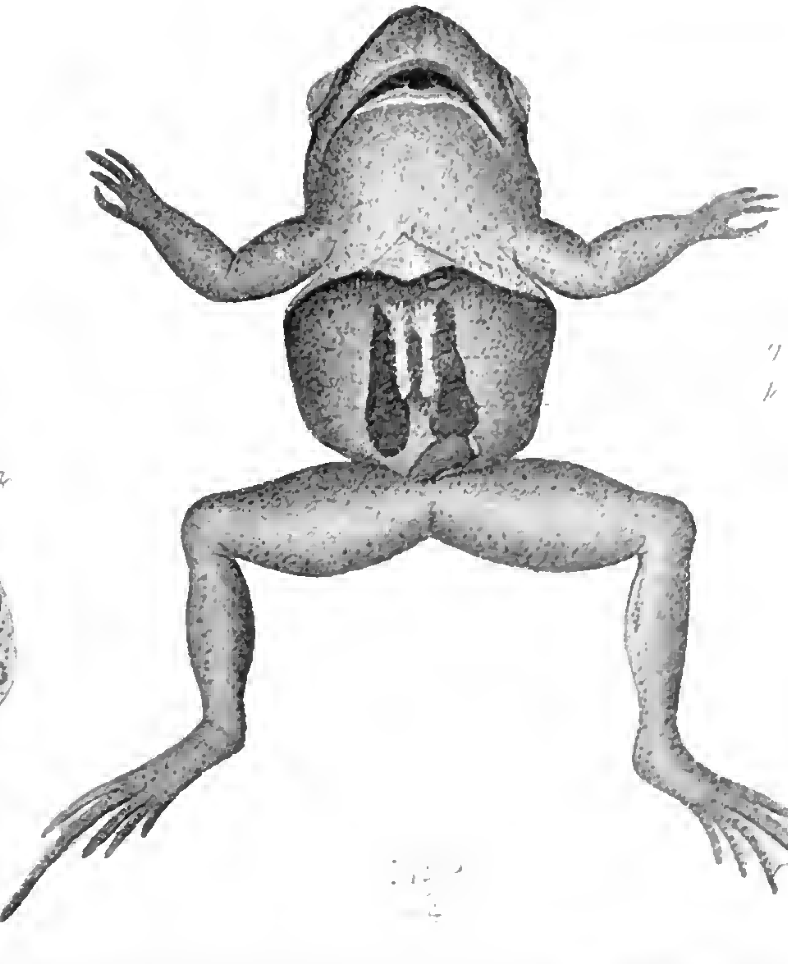


Fig. 6
×60



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Two New Types of Actiniaria.

By

G. Herbert Fowler, B.A., Ph.D.,
Assistant to the Jodrell Professor of Zoology in University College, London.

With Plate XV.

In a bottle of corals, which had been collected from the reefs at Papeete during the expedition of H.M.S. "Challenger," and sent to me by Mr. John Murray for investigation, I was fortunate enough to meet with three small specimens of an Actinarian, which differs so markedly from all known types, that it will apparently necessitate in the future the formation of a new tribe of Actinaria, of equal value with the Hexactiniæ, Edwardsiæ, Cerianthéæ, &c. From the study of such an isolated form, it is naturally impossible to deduce a satisfactory definition for either tribe, genus, or species. I will therefore leave this omission to be filled up by future observers of allied forms, and merely describe the anatomical characteristics in order. I propose for the animal the name

THAUMACTIS MEDUSOIDES, gen. sp. nn.

Of the three specimens at my disposal, the largest was about 2·5—3·0 mm. in diameter, the second about 2·0—2·5 mm., and the smallest 0·8 mm.; and, while the two larger were in a state of contraction (fig. 1),[1] the smallest (fig. 2) was fairly

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[1] Figs. 1 and 2, though carefully drawn with camera lucida under reflected and transmitted light, were seen, on the study of sections, to be inaccurate in some points, such as the exact number of the tentacles. In cases of discrepancy between these two figures and the text, the latter is therefore to be followed.

well expanded. The whitish-yellow colour of the specimens is to be attributed merely to preservation in alcohol.

The animal is flattened in shape, and almost medusiform; it appears to be free-swimming (? crawling), for the aboral ectoderm is entirely similar to that of the oral surface, and shows no trace of attachment, past or future, to any foreign body. From the biconvex shape, it follows that there is no true body wall (mauerblatt, colonna), but the animal is divisible into oral and aboral surfaces. Of these, the oral surface is beset irregularly with what I shall term pseudo-tentacles, since neither in number, position, nor structure can they be regarded as homologous with true tentacles (fig. 1). In the expanded specimen (fig. 2) fourteen true tentacles surround the stomodæum, and peripherally to them are seen the earliest buds of the pseudo-tentacles; but in retracted specimens (fig. 3) the true tentacles, together with the stomodæum, are drawn downwards and outwards into the coelenteron. From the regularity and symmetry with which this is effected in both cases, it is evidently the normal mode of retraction, and is not due to death struggles or alcoholic contortion.

The aboral surface is covered by a single layer of columnar ectodermal cells, which are shortest at the centre of the disc, and lengthen towards the circumference, at which the two surfaces meet in an acute angle. The oral surface is histologically identical with the aboral, but bears the pseudo-tentacles scattered irregularly over its surface to within a short distance of the bases of the true tentacles. The point at which the pseudo-tentacles cease marks the boundary of that part of the oral disc which is drawn inwards and downwards in retraction by the action of the sphincter muscle.

The pseudo-tentacles, three stages in the growth of which are shown in fig. 4, arise each as a simple hollow outgrowth from the coelenteron, in which all three body-layers take part (fig. 9). The bud extends laterally over the surface into three or four "roots," and is continued upwards as a free, finger-like process (fig. 4). The cavity is nearly obliterated by the presence of great numbers of zooxanthellæ. The ectoderm on the apices of the "roots" is generally well supplied with nematocysts, that of the finger-like process is simple and devoid of nematocysts when present, but in the older specimen it has generally disappeared, leaving the mesoglœa bare. On the latter a slight musculature is generally recognisable, but is not sufficiently strongly developed for a determination of its origin and direction; it probably agrees with that of the rest of the animal. From the true tentacles these structures are to be distinguished by their shape (the presence of the "roots"), by the absence of nematocysts on the motile finger-like process, and by the fact that they are irregularly distributed, bearing no relation to the mesenterial chambers either in number or in position, but appearing in all stages of formation in the neighbourhood of a single mesenterial chamber (fig. 4).

The true tentacles are set on the boundary between oral disc and stomodæum. In the largest specimen they were twenty in number, i.e. one to every pair of mesenteries, with one exception. In the smallest specimen fourteen were present as against eleven pairs of mesenteries. They are perfectly normal evaginations of the intra-mesenterial chambers (entocœles); their ectodermal layer is slightly marked off into batteries of nematocysts, most obvious in longitudinal sections. The ectodermal longitudinal muscle is well developed, the endodermal circular layer much weaker. No pore is present at the tip of the tentacle.

The stomodæum, which follows immediately on the tentacles, in the expanded specimen occupies the usual position, but in the contracted examples is turned upwards and inwards in the remarkable manner represented in fig. 3, *st.* It is covered by a single layer of deeply-staining columnar ectodermal cells. No siphonoglyphe is recognisable on it at any point, in either the expanded or contracted specimens.

The musculature of the general wall of the body is for the most part very slightly developed, but may be recognised as consisting of an endodermal concentric (circular) layer, and of an ectodermal radial (longitudinal) layer. As Prof. Hertwig has pointed out ('Chall. Rep. Zool. Actiniaria,' Supplt., p. 12), the occurrence of the latter muscle-layer on the "mauerblatt" is confined to Corynactis and Cerianthus among the Anthozoa, but is characteristic of both hydriform polyps and Scyphistomæ among the Hydrozoa. As there is no reason to believe that Thaumactis is derived from an Actinian-like ancestor with a "mauerblatt," the presence of this ectodermal longitudinal muscle is of considerable phylogenetic interest. Both sets of muscles are extremely weak, and consist merely of single parallel fibrils, which produce a slight unevenness of the mesoglœa lamina.

In two regions, however, of the wall of the body, these muscles attain to a more considerable development, namely, on the indrawn part of the oral surface, and on the stomodæum. On the ectodermal side of the mesoglœa in both these regions are developed longitudinal muscle-fibres, adhering to pleatings of the mesoglœa (fig. 5), by which the expansion of the animal is doubtless effected. On the endodermal side of the invaginated part of the oral surface occurs a strong circular muscle, forming a true sphincter of the "diffuse" type; in the contracted condition, this is continuous from the bases of the tentacles right on to the horizontal surface, where it passes into the general circular muscle; it is the chief muscle concerned in the invagination of the disc during retraction. The endodermal circular musculature of the stomodæum is very slight, its function being merely to close the entrance into the coelenteron during digestion. The musculature of the tentacles has been noticed in connection with them.

The mesenteries amounted in the largest polyp to twenty-one pairs, of which one pair only were directive mesenteries. Of the total number, six pairs (including the directive) are "primary," and are attached along the whole length of the stomodæum; six are "secondary," of which those four only which lie nearest to the directive meet the uppermost (in the expanded state) part of the stomodæum; while the nine pairs of tertiary mesenteries are developed chiefly in the neighbourhood of the directive pair, and do not touch the stomodæum at any point. Their arrangement, beginning with the directive pair is as follows: 1, 3, 2, 3, 1, 3, 2, 3, 1, 2, 1, 3*, 2, 1, 3, 2, 3, 1, 3, 2, 3. Over each pair of mesenteries is placed a tentacle, with the exception of the pair marked above with an asterisk, the position of which suggests that it was more recently developed than the rest. Muscles are present on both faces of the mesenteries; those on the outer (ectocœlic) aspect are the protractors, and are recognisable in transverse section only at the upper part of the mesentery (fig. 5). Their function is to assist the ectodermal longitudinal muscles of the oral surface and stomodæum in the expansion of the animal. Those on the inner (entocœlic) aspect are the retractors, by which a general contraction is effected, and the stomodæum pulled upwards and inwards; they are indicated in fig. 3 by faint lines on the mesentery.

The free edge of the mesentery is not thrown into much contortion, and for the most part bears the normal form of filament (fig. 7). Besides this, however, occurs on most mesenteries a structure, which I can neither describe nor figure with any accuracy, owing to scantiness of material and imperfect preservation. In transverse section of the polyp it sometimes presents the appearance represented in fig. 8, but more often appears as a solid swelling on the edge of, or in the centre of, the mesentery. Above and below it the ordinary form of filament often occurs. A number of these structures were extremely obvious when the larger specimen was stained and cleared (fig. 1), they then presented a gastrula-like appearance.

In the smallest specimen, eleven pairs of mesenteries were present, of which the rather larger six pairs are primary, the remaining five secondary. No directive pair is present. The number of tentacles (fourteen) would seem to indicate that, as is often the case, the addition of new cycles of mesenteries is to a certain extent preceded by multiplication of the tentacles. The mesenteries essentially agree with those of the larger specimen, except for the fact that they do not exhibit the peculiar form of (?) filament. The contortion of the free edge is proportionately much more considerable than in the larger specimen.

No generative organs occurred in either of the three examples.

It is a matter of regret that this new morphological type does not throw any fresh light on the obscure phylogenetic relationship of the various tribes of Actinaria to each other. Doubtless the non-fixation (cf. the primitive Halcampæ) and persistent biconvex shape of the polyp indicate a condition more or less ancestral, while from the ectodermal, longitudinal (radial) muscle, which characterises hydroid-polyps and Scyphostomæ, Prof. R. Hertwig would infer a very close relation with the Hydrozoa, a conclusion which is certainly strengthened by the shape of the body. A study of the structure of the animal certainly does not suggest that it is a highly modified form derived from representatives of the existing Hexactinian type, but rather that it is collaterally descended from an ancestor represented by the somewhat flattened larva of modern Anthozoan embryology, with no distant kinship to the Hydrozoa. From existing forms, Thaumactis is marked off by the pseudotentacles, the method of retraction, the abnormality of the directive mesenteries, the biconvex shape, and the ectodermal radial musculature; and may possibly stand as type of a new tribe, the Thaumactiniæ.

PHIALACTIS NEGLECTA, gen. sp. nn.

Of this new Actinian, two broken examples were found in the same bottle with the Thaumactis described above, attached to pieces of Millepora sp. from the Papeete Reefs. Its claim to interest lies in the fact that it affords a further example of that retrogression of the tentacles, of which the only known examples are four genera of Hexactiniæ, and two Paractiniæ, all occurring among the deep-sea "Challenger" Actiniaria described so ably by Prof. R. Hertwig. From these, however, this new genus differs in the fact that the tentacles are replaced, not by stomidia—slight elevations of the oral disc, surrounding a large opening which is homologous with the pore at the tip of some normal Actiniarian tentacles—but by what I will term sphæridia, i. e. ampullate diverticula of the inter- or intra-mesenterial chambers, devoid of an opening to the exterior, and homologous, therefore, with the imperforate tentacles of many genera.

This difference appears to necessitate the formation of a new family of Hexactiniæ, the Phialactidæ, which will rank beside the Liponemidæ, and may be defined as "Hexactiniæ, in which the tentacles have degenerated into sphæridia." The possibility, however, must be borne in mind that Phialactis may belong, not to the Hexactiniæ, but to the Monauleæ (should such a group prove to be natural), since in the one specimen of which transverse sections were made, only one pair of directive mesenteries could be detected with certainty (cf. p. 150). With the single form only at disposal, it is better to abstain from even a provisional definition of genus and species.

The animal is goblet-shaped, the cup being represented by an upward extension of the oral disc, the stem by the body of the animal, and the foot by the limbus or base of attachment (figs. 10, 11). The sphæridia are borne on the inside of the cup only, and are especially numerous round the oral cone. The latter lies at the bottom of the cup, and does not itself bear sphæridia, in its centre lies the oval entrance to the stomodæum (fig. 12).

The external dimension of the most perfect specimen are approximately as follows:

Total height	6 mm.
Height from limbus to oral opening . . .	2 ,,
Height from oral opening to upper edge of cup .	4 ,,
Diameter of cup above	10 ,,
Diameter of cup below (outside)	7 ,,
Diameter of body	6 ,,
Diameter of limbus	10 ,,

The general structure agrees with that of an ordinary Actinian, the abnormal shape being produced merely by a considerable upward growth at the point where body wall (mauerblatt) passes into oral disc. The outer part of the cup thus formed is to be regarded, therefore, as belonging to the former, the inner side, which carries the sphæridia, to the latter. The structure of the cup can be gathered from the schematic figure 14 without further description. The thickness of the mesoglœa appears to be characteristic of the whole animal.

The sphæridia, the degenerate representatives of the tentacles, call for little remark; they are hemispherical ampullæ (figs. 13, 14, *sph.*), scattered irregularly over the oral disc, communicating by a passage narrower than their diameter, with either inter- or intra-mesenterial chambers. No distinction into cycles is possible, no special musculature is recognisable. In a specimen not figured they were rather more numerous than in fig. 12, and set more regularly in rows corresponding to particular mesenterial chambers. They are covered by simple columnar epithelium, are devoid of nematocysts, and present no terminal pore.

The stomodæum exhibits a slight structural variation from the normal type; it is marked internally by a series of tongue-like ridges produced by inward growth of the mesoglœa and ectoderm, the endoderm taking no part in their formation (fig. 13). They do not correspond to mesenteries or mesenterial chambers. No siphonoglyphe is recognisable.

The mesenteries in the most perfect specimen amounted to twenty-three pairs, at and below the plane of the oral opening, of which twelve were complete, and comprised the first two cycles, while the remaining eleven pairs may be referred to an incomplete tertiary cycle. Near the lip of the cup, at least fifty pairs were present, so that in this, as in some other genera, new mesenteries take origin just under the oral disc, and not in the angle between body wall and pedal disc.

Only one pair of directive mesenteries could be determined by transverse sections of the most perfect specimen; a second pair was perhaps present, but unrecognisable owing to the slight development of muscle on many of the mesenteries. While in many cases the mesoglœa lamina of the mesenteries is reduced to a thin refringent line, in others it forms, at the plane of the contorted edge of the mesenterial filament, a stout plate, club-shaped in transverse section, and carrying large muscle-fibres (fig. 15). To this, but marked off from it by a sudden change in the thickness of the lamina, is attached the contorted region of the mesentery, provided with more muscle than is generally the case.

The muscle of the body wall and oral disc is endodermal and circular, and is not differentiated into a sphincter at any point.

As is so often the case, nematocysts of two kinds were present, of which the larger measured as much as ·14 mm. × ·044 mm., and were provided with unusually large cnidocils.

In conclusion, I desire to express my thanks to Mr. John Murray, by whose courtesy I am permitted to present an account of these two interesting forms.

Since writing the above description, I have had the great advantage of submitting my drawings to Professor R. Hertwig, who inclines to the opinion that Phialactis should be associated with the Corallimorphidæ. While it is probable that a parallel retrogression of the tentacles has taken place in more than one family simultaneously, it will perhaps be best, till the steps in the process are known, to allow the Phialactidæ to stand near the Liponemidæ, although the genera in both families may be eventually found to be merely degenerate representatives of other existing families.

EXPLANATION OF PLATE XV,

Illustrating Dr. G. Herbert Fowler's paper on "Two New Types of Actiniaria."

FIGS. 1—9.—THAUMACTIS MEDUSOIDES, gen. sp. nn.

Fig. 1.—The largest specimen, retracted; from the oral aspect. While the rest of the polyp has been drawn by transmitted light, the pseudotentacles scattered over the surface are, for clearness' sake, represented as if under reflected light. Compare with this fig. 3. The clear space

in the centre is the opening to the cœlenteron, left on invagination of the oral disc; the dark ring surrounding it is produced by the inverted stomodæum, &c.; and from this the true tentacles radiate outwards, among the mesenteries. × 30.

Fig. 2.—The smallest specimen, expanded; viewed from the oral surface. Round the true tentacles (*cf.* note, p. 143) are seen the budding pseudo-tentacles. × 50.

Fig. 3.—Diagram of a vertical section of the contracted polyp, from a camera lucida drawing. *te.* The true tentacles. *ps. t.* The pseudo-tentacles. *st.* The inverted stomodæum. *mes.* The mesenteries. × 30.

Fig. 4.—Portion of the oral disc, showing three stages in the development of the pseudo-tentacles. × 47.

Fig. 5.—Transverse section through the invaginated oral disc and stomatodæum at the base of a tentacle in a contracted specimen. The arrow indicates the plane of section in Fig. 6. The pair of mesenteries exhibit the protractor exocœlic muscles in transverse section (compare their trend in Fig. 3). The laminated cuticle external to the ectoderm is probably only a mucous secretion. × 210.

Fig. 6.—Vertical section through the invaginated oral disc and stomatodæum, *i.e.* an enlargement of part of Fig. 3. The arrow indicates the plane of section in Fig. 5. × 210.

Fig. 7.—Transverse section of normal mesenterial filament. × 210.

Fig. 8.—Transverse section of (?) abnormal mesenterial filament. × 210.

Fig. 9.—Section through the root of a pseudo-tentacle. The endoderm is completely obscured by zooxanthellæ. The endodermal circular muscle of the wall of the body is well seen. × 210.

Figs. 10—16.—Phialactis neglecta, gen. sp. nn.

Fig. 10.—Lateral view of the polyp. × 3.

Fig. 11.—Diagrammatic longitudinal section of the polyp, showing the position of the oral opening at the bottom of the cup. × 3.

Fig. 12.—View of the cup from above. × 3.

Fig. 13.—Schematic transverse section through the base of the oral cone. *sph.* Sphæridia. *st.* Stomodæum. *m.* Mesentery. × 32.

Fig. 14.—Schematic transverse section through a part of the cup. *sph.* Sphæridium. *or. d.* Inner or oral disc surface. *b. w.* Outer or body-wall surface. *m.* Mesentery. × 47.

Fig. 15.—Transverse section of a mesentery (p. 150). × 62.

Fig. 16.—Nematocyst of the larger kind, with cnidocil. × 210.

Fig. 1.

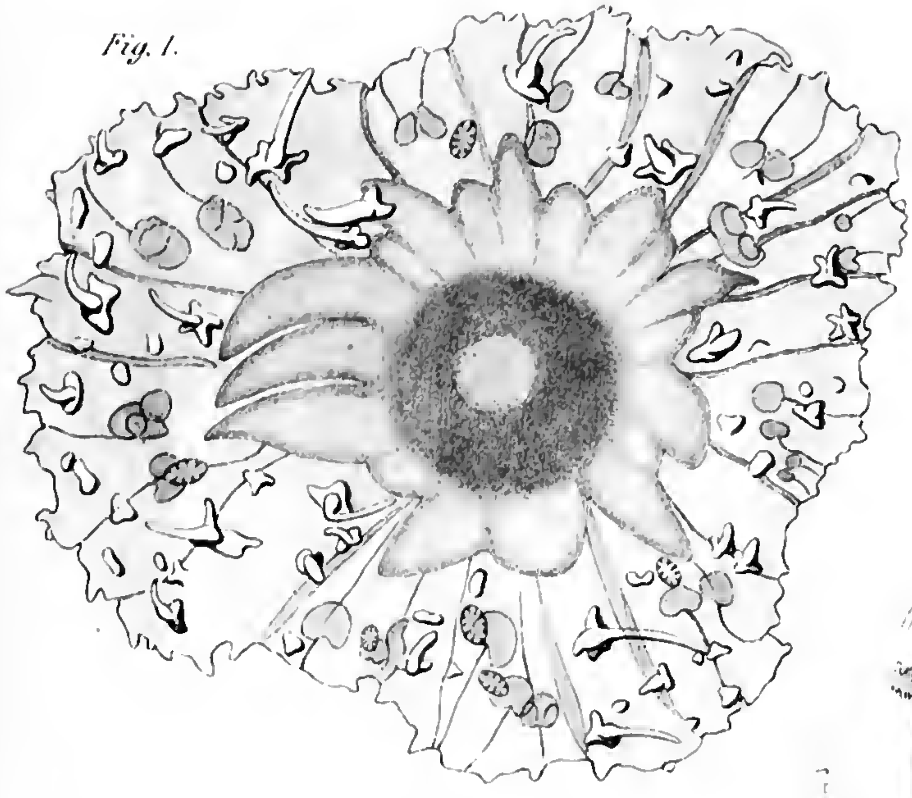


Fig. 2.

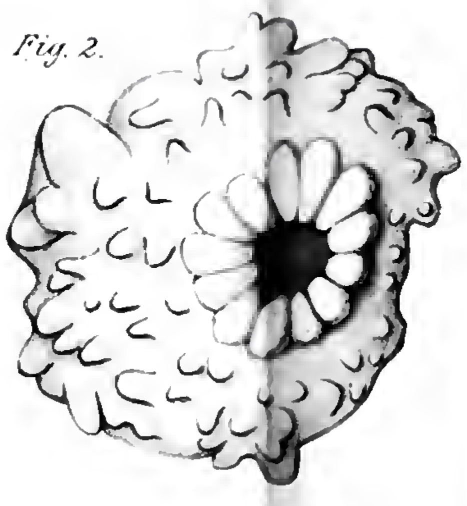
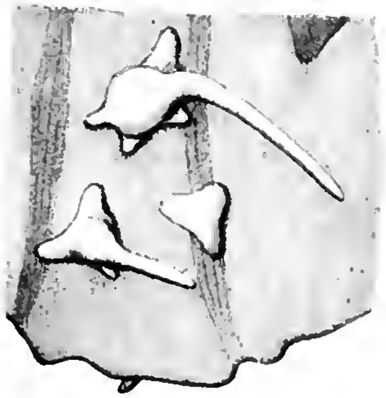


Fig. 3

Fig. 4



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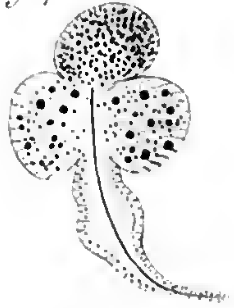

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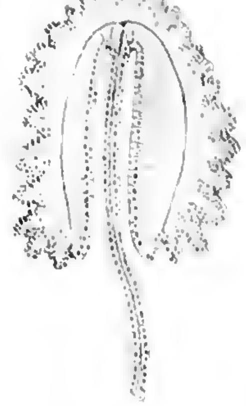

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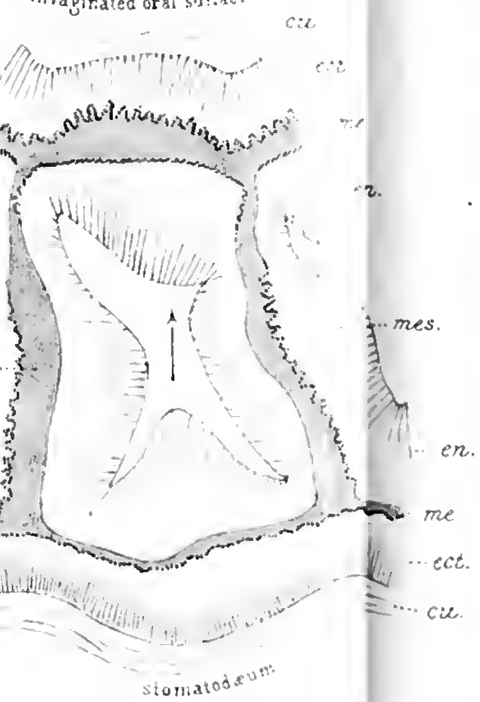

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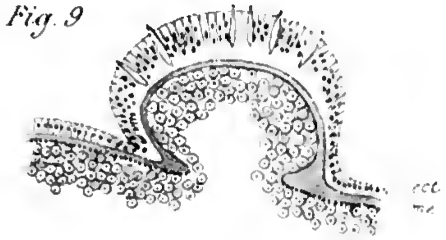

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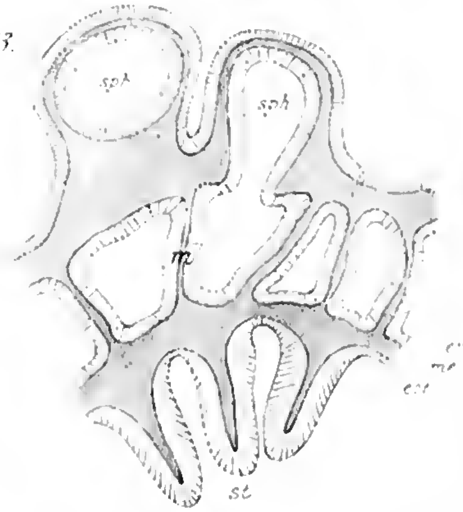

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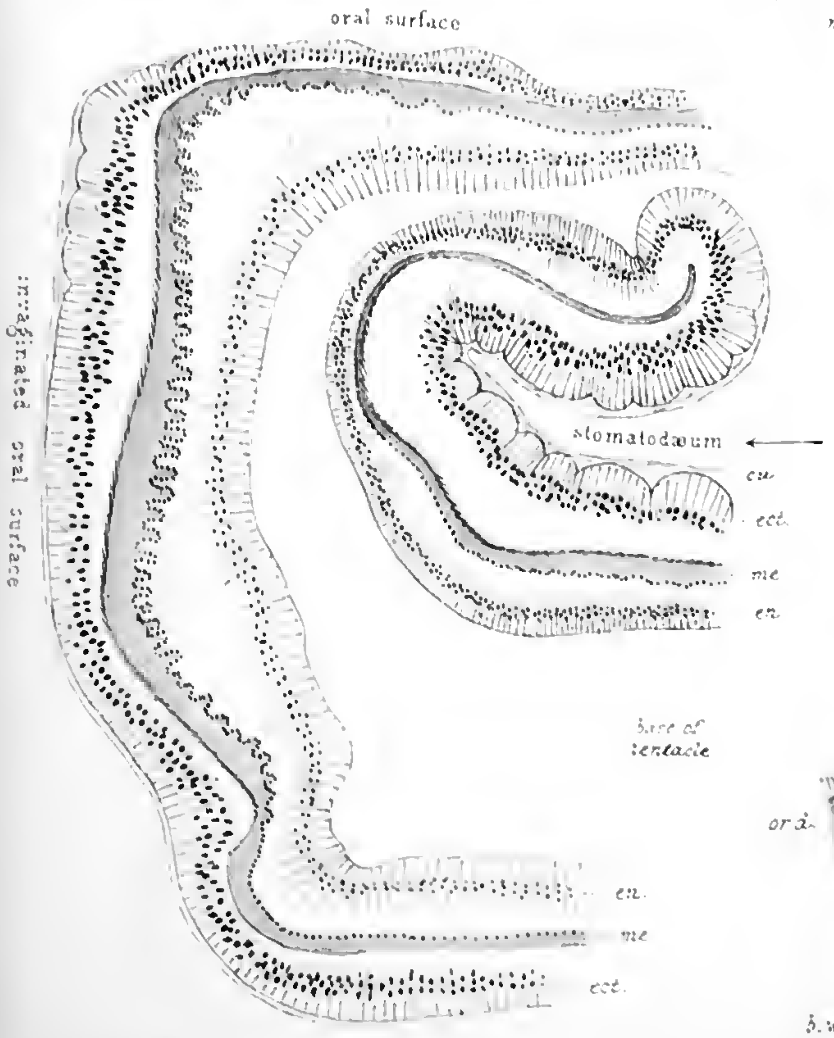

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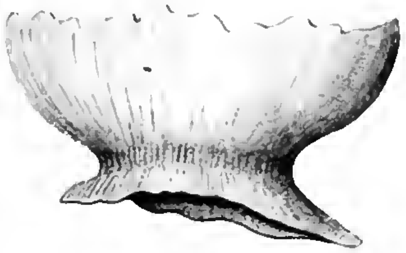


Fig. 16

Fig. 14.

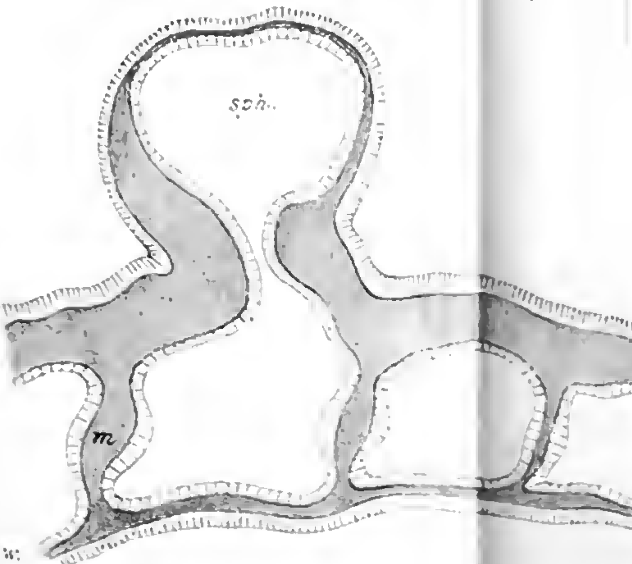


Fig. 11

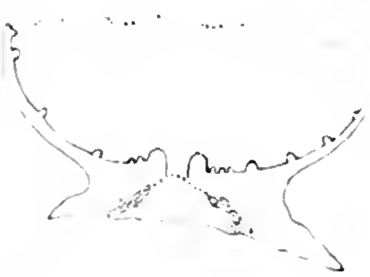
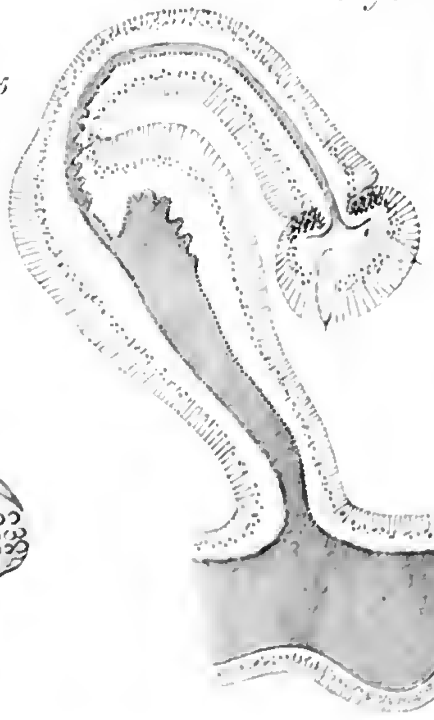


Fig. 15



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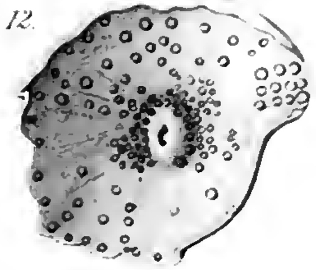

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Morphological Studies.

II.—The Development of the Peripheral Nervous System of Vertebrates.

Part I.—ELASMOBRANCHII AND AVES.

By

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With Plates XVI, XVII, XVIII, XIX, XX, XXI.

TABLE OF CONTENTS.

The researches recorded in the following pages were undertaken in consequence of a grant for the purpose made from the Government fund by the Grant Committee of the Royal Society.

INTRODUCTION.

Nearly three years ago I published (No. 6) in the pages of the 'Quart. Journ. of Micr. Sci.,' some researches on the morphology and development of the so-called "organs of the lateral line," which appeared to me then, as now, to be in reality special branchial sense organs. When those researches were first undertaken in Professor Semper's laboratory (No. 4), it was far from my intention to investigate the development of the cranial nerves and ganglia, but in the course of the work it soon became obvious that the thorough study of those sense organs could only be accomplished by including the cranial nerves and ganglia in the sphere of the observations. And, indeed, almost the first Elasmobranch embryo examined showed unmistakeably that the cranial ganglia and the sense organs of the lateral line are intimately associated in their morphology and development.

The researches then published include also attempts to homologise the sensory portion of the nose and ear with the sense organs of the lateral line. And it is partly with the wish to get more light on this question that last year I undertook the investigation of the first beginnings of the cranial and spinal ganglia. Two papers—very different in their stimulating effects—urged me all the more to a thorough study of these problems.

In a short notice Dr. van Wijhe (No. 61)—whose right to an opinion on this matter is unquestionable—considered his researches on Ray embryos entitled him to combat my previously published views of the nature of the nose. I give in the following lines van Wijhe's own words.

He says: "Die Auffassung nach welcher der Olfactorius ein segmentaler Nerv sei, ist neulich wieder von Dr. Beard vertreten. Er gründet dieselbe auf die Theilnahme der Epidermis an der Bildung des Reichnerven und seines Ganglions, wie dies auch bei den Nerven der Seitenorganen der Fall ist und glaubt die Reichgruben seien deshalb den Seitenorganen und der Olfactorius den Nerven dieser Organe homolog.

. . . . . "Ich finde dass der Olfactorius zu Anfang von Balfour's Studium I noch nicht vorhanden ist; er tritt erst zu Anfang der Periode J auf, wann die vierte Kiementasche schon angelegt, aber noch keine nach aussen durchgebrochen ist. Das Riechorgan und der Nerv enstehen beide aus dem vorderen Neuroporus. Der Olfactorius entwickelt sich nicht aus der Nervenleiste, denn er tritt in einer Periode auf, wann dieselbe im Kopfe schon längst geschwunden ist; auch ist er von Anfang an mit der Haut in Verbindung, und unterscheidet sich durch diese zwei Merkmale von allen übrigen dorsalen Nervenwurzeln." . . . . .

. . . . . "Dass nun die Zellen der Anlage des Riechorganes an der Bildung des Nerven und seines Ganglions theilnehmen ist, wie mir scheint, bei einer solchen Enstehungsweise a priori zu erwarten, und stimmt mit der Nervenbildung bei vielen Wirbellosen überein."

. . . . . "Wenn Beard jetzt, seiner früheren Behauptung entgegen, den Olfactorius und die Seitennerven nebst ihren Ganglien allein aus der Epidermis enstehen lässt, so kann er dies wohl nie beweisen, weil der Stamm der Nerven sich ursprünglich aus dem Medullarrohre entwickelt."

The above statements relate to some of the most important problems in the development of the peripheral nervous system. And if the whole of them are to be maintained in van Wijhe's sense they present insuperable difficulties in the way of the acceptation of my previous interpretations. To me the most serious question then, and before then, was the nature of Marshall's neural ridge and its supposed origin as an outgrowth of the central nervous system. If I had left it entirely untouched in my previous work, such a proceeding can be easily excused. In the first place, my material did not then appear to me sufficient to settle the matter, and the complete study of the "neural ridge," &c., required more time than I could then devote to it. Further, I could not without ample justification declare Marshall's account and that of Balfour to be at the basis erroneous. And when Professor Gegenbaur, in his recent work (No. 21, p. 42), makes me the reproach that I never entertained the question of the epiblastic origin, apart from the central nervous system, of the neural ridge, the accusation is unjust; for I can assure Professor Gegenbaur that such was far from being the case.

And, as it now turns out, van Wijhe's objection that the main root of the nerve arises as an outgrowth of the central nervous system will not hold, for the origin of what he calls the main root, in the case of the cranial and spinal ganglia, is demonstrably in principle in accordance with the account of the development of the olfactory nerve and ganglion, as given by van Wijhe himself. In fact, in the main, I accept gladly and gratefully van Wijhe's researches on the olfactory organ as supporting and confirming my view of its homology. But for a fuller discussion of this matter, I must ask the reader to wait till the ground has been cleared by the detailed account of the researches on the very first origin of the cranial ganglia in nearly all classes of Vertebrates.

And now a few words on the second work, which was the great stimulating agent in impelling the researches about to be recorded. If the reader will refer to the introduction of my work on the branchial sense organs (No. 6) he may read that "at present we are acquainted with no Invertebrate nervous system which is built on the same plan as that of Vertebrates." This conclusion led me to take up an attitude of expectancy rather than of negation towards the Annelidan theory of the origin of Vertebrates. And while I felt compelled to doubt the homology between the "Seitenorgane" of the Capitellidæ and the "Seitenorgane" of Vertebrates, so ably maintained by Eisig, I was not quite without hopes that further researches on Invertebrates might reveal facts on which a comparison of the peripheral nervous system of Vertebrates, with some allied stock of Invertebrates, probably Annelids, might be maintained.

In October, 1886, appeared Kleinenberg's epoch-making researches on the development of Lopadorhynchus (No. 41). I shall find plenty of opportunity in this and some of the following studies for reference to this remarkable paper, and will here only quote one passage, which may serve as a text for the researches I am about to record.

He writes (p. 219): "Die grössten Schwierigkeiten bietet der Vergleich des Centralnervensystems der Wirbelthiere mit dem der Anneliden. Zunächst der Umstand, dass bei den ersteren eine durchaus einheitliche Anlage für Rückenmark und Gehirn vorhanden zu sein scheint. Dies könnte durch eine allmählich eingetretene und schliesslich mit den ersten Bildungsvorgängen zusammen fallende Verschmelzung der umbrellaren und sub-umbrellaren Abschnitte des Anneliden-systems erklärt werden, dann bliebe immer noch zu bestimmen, welcher Theil dem ursprünglichen Kopfganglion entspricht. Das ganze Gehirn gewiss nicht. Seine bei weitem uberwiegende Masse stammt offenbar vom Rumpf her; in ihm fliesst eine Anzahl von Ganglien zusammen, die wohl nur auf die sub-umbrellare Anlage zu beziehen sind. Die Hoffnung, auch bei den Wirbelthieren eine gesonderte Anlage, welche dem Kopfganglion der Anneliden gleichwerthig wäre, zu finden, ist etwas kühn. Wenn nicht wahrscheinlich bleibt immerhin möglich, dass das ursprüngliche Kopfganglion ganz unterdrückt, und von den vorderen Theile der Bauchkette substituirt worden ist. Denn weniger resolut als Dohrn, Semper, und andere, bin ich doch geneigt mit ihnen die Homologie des Rückenmarks der Wirbelthiere und des Bauchmarks der Anneliden anzunehmen. Schon vorhin sprach ich die Vermuthung aus, dass der Primitivstreifen einem Theil der sub-umbrellaren Neuromuskelanlage entspricht. Es erscheint mir als ein grosses Verdienst Kölliker's, fast allein den ectodermalen Ursprung des Mesoderms an dieser Stelle festgehalten zu haben, ohne sich von dem lauten Widerspruch beirren zu lassen. Natürlich trete ich allen denen entgegen, welche in der Primitivrinne weiter nichts als ein Uberbleibsal des Blastopors sehen; eine gewisse Beziehung zu demselben verträgt sich aber auch ganz gut mit meiner Auffassung.

"Das bleibende Rückenmark würde dann vielleicht nur den vorderen Abschnitt der ursprünglichen Anlage enthalten. Der

Weg den die parallelen seitlichen Stränge des Bauchmarks durchlaufen haben müssen, um zum medianen Rückenmarksrohre zu werden, scheint mir durch die mitgetheilten Thatsachen aus der Entwickelungsgeschichte der Anneliden selbst hinreichend klar vorgezeichnet.[1] Noch mehr. Auch die Spinalganglien dürften ihre Homologie bei den Anneliden finden, und zwar in den Parapodialganglien. Dreht man die fig. 47, Taf. xi,[2] um, so wird die Uebereinstimmung nicht entgehen. Der Unterschied liegt nur darin, dass die Spinalganglien bei ihrem Auftreten dicht am Rückenmarksrohr liegen oder in dasselbe eingezogen sind. Die hintere Wurzel—das am besten gekannte Beispiel der Enstehung eines Nerven bei den Wirbelthieren—bildet sich gerade so wie der mediane Parapodial Nerv, und die vordere Wurzel dürfte dem Muskelnerven, der sich mit jenem zu einem Stamm verbindet, gleich zu setzen sein."

So much for the present from Professor Kleinenberg. In general terms the result of my researches is a confirmation of his views and comparisons.

If any further excuse were needed for a reopening of the question of the origin of the ganglia in Vertebrates, one would not have to seek far for ample reasons for such a course. Just as I was completing the first part of this work, three publications appeared, all of which showed the state of uncertainty and vagueness in which these questions at present exist. Professor Gegenbaur (No. 21) has undertaken no investigations on the matter, but feels himself entitled to quote as final the observations of one or other of his pupils, those of Sagemehl (No. 56) more especially appear to him to be far away above suspicion. I shall later on have occasion to point out how

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[1] In a subsequent paper I intend to demonstrate that the central nervous system is a paired structure which arises as two lateral plates of neuro-epithelium separated by a median ciliated groove, just as in Annelida.

[2] I have reproduced this figure in Plate XIX, fig. 64. In my copy the figure has been turned through an angle of 180°, to bring it in the "Vertebrate position."

little claim Sagemehl's researches on the spinal ganglia really have to pose as a solution of the prize problem they were undertaken to solve, and will here content myself with the assertion that Sagemehl never saw any of the very earliest stages of development. Professor His (No. 34) in a paper, which in spite of a vast number of differences of opinion as to both facts and hypotheses, I cannot regard otherwise than as a valuable contribution to the morphology of the cranial nerves, has, among other things, endeavoured to establish without further observation his celebrated "Zwischenrinne" or "Zwischenstrang" theory, and he believes that all that is necessary for its final triumph is its rebaptism under the name of Ganglienrinne or strang. As this work also will occupy our attention for some time at a later stage of the work, I will only express my strong dissension with the following extract (p. 380) with which Professor His opens his campaign against "die jüngeren vergleichendmorphologischen Schulen." It reads thus: "Bei genauerem Zusehen findet man eben dass die Differenzen nicht in dem liegen, was der eine oder der andere Beobachtungskreis an thatsächlichen Befunden ergiebt, sondern in demjenigen was die Vertreter der einen und der andern Schule zwischen den Zeilen zu lesen sich bemühen."

It will be time enough to consider the lecture which Professor His reads to us younger morphologists, when the facts of development which form the very basis of the question are placed beyond the reason of dispute. The principle of the origin of the ganglia from the epiblast, apart from the central nervous system, is one on which I can agree with Professor His. Not so with the way in which this takes place; for, paradoxical though it may sound, right as Professor His was in principle, he is till now further from recognising the true facts than any embryologist who has worked on the origin of the peripheral nervous system. Sad to relate the Zwischenstrang, &c., has as little direct connection with the origin of the ganglia as it has with the urinogenital system, as Professor His at first supposed.

Professor His is astonished to notice that his views on this matter have been "völlig unbeachtet," and finds,—though this discovery is not likely to be accepted by anyone competent to judge the question,—that his original views are practically identical with the generally accepted account of Balfour.

Now, among those naturalists who have worked on the development of the peripheral nervous system, Balfour stands pre-eminent in the precise formulation of his conclusions. I am bound to maintain that on many of the most fundamental questions Balfour's observations cannot be longer upheld, while I am also sure that none would be more ready than he to accept the facts I am about to record.[1] Balfour says (No. 2, p. 369): "All the nerves are outgrowths of the central nervous system." How this statement can be reconciled with his Zwischenrinne hypothesis (for it is nothing more than an hypothesis) it is for Professor His to determine. The matter need not trouble us much, for, as I shall afterwards show, the Zwischenstrang (there is no Zwischenrinne!) is just that portion of the epiblast or ectoderm which takes no part at all in the ganglionic formation. All I here wish to do is to enter a protest against the way in which Professor His attempts to convert all previous work on the early development of the ganglia into a mere confirmation of his own more or less

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[1] It is certain that Balfour had an idea of the true facts, for he closes his account of the peripheral nerves on page 383 of the 'Comparative Embryology,' vol. ii, with this passage: "Situation of the dorsal roots of the cranial and spinal nerves. The probable explanation of the origin of nerves from the neural crest has already been briefly given. It is that the neural crest represents the original lateral borders of the nervous plate, and that, in the mechanical folding of the nervous plate to form the cerebrospinal canal, its two lateral borders have become approximated in the median dorsal line to form the neural crest. The subsequent shifting of the nerves I am unable to explain, and the meaning of the transient longitudinal commissure connecting the nerves is also unknown. The folding of the neural plate must have extended to the region of the olfactory nerves, so that, as just stated, there would be no special probability of the olfactory nerves belonging to the same category as the other dorsal nerves, from the fact of their springing from the neural crest." The reader may compare the first sentences of this passage with the results recorded in the following pages.

hypothetical views on this matter. That the Zwischenstrang has any concern in the formation of the ganglia is a baseless assumption.

In his 'Lehrbuch der Entwickelungsgeschichte,' &c., Bd. ii, Professor O. Hertwig has made an attempt to extract a little light from the chaos which reigns over our knowledge of the development of the peripheral nervous system. For Professor Hertwig, the most important researches are those made by his pupils and by Sagemehl. As he mainly relies upon these and ignores for all practical purposes almost entirely the more recent work on the matter, it is not unnatural that the chapter on the peripheral nervous system is one of the most unsatisfactory in the whole work. As an instance of Professor Hertwig's treatment of recent authors, I may mention that for him our knowledge of the formation of the lateral nerve of Amphibians and Silachians is confined to the older observations of Semper and Goette, and he only mentions incidentally that van Wijhe has seen similar fusions of epiblast and sensory nerves in the head of Elasmobranchs (No. 23, p. 338).

Professor Hertwig has thought fit to illustrate his account with one or two figures from as yet unpublished researches of Professor Rabl. If Professor Rabl is to pose as an authority on the formation of spinal ganglia, one may at least ask for tolerably correct figures in illustration of his work. The two figures 175 and 171 given by Hertwig are among the most incorrect that have been published till now on this matter. As the climax to Professor Hertwig's appreciation of work on the peripheral nervous system, let me add that he is of opinion that "um auf dem schwierigen Gebiete vorwärts zu kommen, muss man . . . . bei der Untersuchung von Embryonen nicht nur Schnittserien, sondern auch andere histologische Methoden zu Rathe ziehen" (p. 337). It is to be hoped that besides giving the advice Professor Hertwig will also show us the way to use his "andere histologische Methoden." From these citations the reader will, I think, be convinced that from the researches till now published, we may form very different conceptions of the results obtained according as one belongs to this that or the other school of embryologists. For myself, for the better comprehension of my work on later stages, it was absolutely essential that a clear, precise, and uncontradictory account of the very first stages of the peripheral nervous system, and of the relations of the latter to the central nervous system, should be worked out. It was necessary to attempt to do for the Vertebrate nervous system what Kleinenberg has done for that of the Annelid. Not that the following researches make any pretence to being an account comparable in minuteness of detail with Kleinenberg's work, they are rather the beginnings of work on the matter; for there is still much to be done in the early development of both central and peripheral nervous systems of Vertebrates.

According to Professor Wiedersheim's opinion and my own, the most lasting results were likely to be obtained by drawing within the sphere of investigation as many types of Vertebrates as possible, and hence, although my original intention regarding this and other researches was to consider only Elasmobranchs and Ganoids, in aid of which researches the Government Grant Committee of the Royal Society of London made a grant of money from the fund at their disposal, I nevertheless thought it in the interest of science to extend my observations to various classes of Vertebrates. So far I have had at my disposal embryos of (various genera) Elasmobranchs, Teleostei, of Amphibia, Reptiles, Birds, and Mammals. Researches on Ganoids[1] and one or two other types as yet unattainable, I hope in the course of the year to be able to carry out. For the moment in consequence of the time necessary for the preparation of the numerous indispensable drawings, I publish the results obtained on Elasmobranchii and Birds.

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[1] The development in Ganoids conforms exactly to those in other types.

ELASMOBRANCHII.

The researches on this group were made on embryos of Torpedo ocellata, Pristiurus melanostomus, Acanthias vulgaris, Mustelus lævis, and Scyllium canicula. Of the first-named form especially a very large and complete series of stages was at my disposal. This genus, Torpedo, is, in my experience, the best suited for researches on the early development, for the cell elements are larger, and the appearances presented in sections much clearer than those of any of the other forms mentioned. Of the other forms a sufficient number of stages was at my disposal to show that there is no essential difference in the development. And, in fact, for both cranial and spinal ganglia of all the Vertebrates which have till now come into my hands, including Teleostei, Rana, and even the Chick, I may with full confidence say that the appearances presented are all easily reducible to one type—to that of the Elasmobranchii.[1] The differences observed in different forms are in reality very slight, and are readily explicable as variations in the time of development. As in the case of other organs, the development may be either retarded or accelerated. As a striking example of the way in which, for instance, the spinal ganglia agree in development in Torpedo and the Chick, I may mention that in sketches of portions of sections of the two forms drawn under high power it is often difficult, if not impossible, to find any differences, even in detail; and if the reader will compare figs. 37 *a*, 42, and 68, 69, he will, I think, find it impossible of his own knowledge to say definitely that the former are figures of Torpedo sections, the latter of Chick sections.

A. Spinal Ganglia of Elasmobranchii.

Balfour is mainly responsible for our knowledge of the development of the spinal nerves and ganglia in Elasmobranchs (Nos. 1, 2, and 3).

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[1] The development in Ganoids conforms exactly to that in other types.

The stages of development which Balfour described as the earliest are, however, by no means such, for I can demonstrate the first traces of ganglia some time before the neural canal closes. Neither Balfour nor Onodi,[1] nor any other observer, has seen the stages which I figure in Pl. XVI, and in figs. 37—42 of Pl. XVIII.

Figs. 1—4 of Pl. XVI are taken from various parts of one embryo of Torpedo ocellata. Figs. 1—3 are the only ones which at the moment concern us, for they are all three from the trunk, and hence from the region of the spinal ganglia.

In Prof. His's recent paper (No. 34, p. 445) the author remarks: "Der Zeitfolge nach entwickeln sich die peripherischen Nerven spät. Am Rumpf treten sei später auf als die Urwirbel, am Kopf fällt die Zeit ihrer Bildung zum nahe an diejenige des Visceralbogen, aber da geht die Gliederung des End-gebietes dem Vordringen der Stämme voraus."

I am not quite sure that Professor His means these remarks also to apply to the ganglia. But however that may be, I will at once assert that the "Anlagen"[2] of the spinal ganglia are formed very much earlier than has hitherto been supposed, and, indeed, that the first traces of them appear when only two or three of the mesoblastic somites[3] have been entirely segmented off from the main mesoblast (figs. 2 and 3). Generally speaking, the first differentiation of the spinal ganglia may be said to occur at about the time of separation of the notochord from the hypoblast. In earlier stages than this fig. 1 (here the

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[1] Onodi's researches, so far as they relate to the posterior root-ganglia of Elasmobranchs after exclusion of the sympathetic, contain no new results And their author was entirely in the dark as to the relations of the ganglia to the lateral sense organs. Though he must have seen the skin fusions he entirely ignores them.

[2] I use the word Anlage or Anlagen (plural) throughout this paper instead of our only term rudiment, which has a double meaning.

[3] In agreement with van Wijhe, Wiedersheim, and others, I use here the word somites, or body-somite, instead of the older and incorrect term protovertebræ. In the same way I shall call the "head-cavities," with van Wijhe, the head-somites. With Dr. Eisig I use the terms hæmal and neural instead of ventral and dorsal.

notochord is already partly separated off) the neural plate is a broad, slightly-grooved, shallow structure, which presents no appearance of differentiation. Very soon the invagination process begins, and with it the Anlagen of the spinal ganglia begin at once to be distinguishable from the rest of the neural plate. At the extreme outer boundary of what is really the "Anlage" of the spinal cord a commencing proliferation of the deeper layers of the epiblast is observable (fig. 2). This leads to the appearance of a bud-like outgrowth of cells at each side of the spinal cord Anlage. On the one hand this outgrowth is very soon sharply distinguishable from the spinal cord Anlage; on the other hand, it begins to separate somewhat from the rest of the epiblast in the form of a somewhat wedge-shaped mass of cells. In figs. 3, 5, 9, this process is readily made out. From an inspection of these figures it will be obvious that the whole thickness of the epiblast is not concerned in this outgrowth. The outer layer of epiblast is quite indifferent, and neither takes share in the Anlage, nor presents any resemblance at all to a sense epithelium, a point on which I shall have more to say in connection with Dr. Eisig's comparisons. The epiblast in the region of the ganglionic Anlage, and for some distance lateral of this, is composed of several cell layers (fig. 1). Now, the way in which the ganglionic Anlage separates from the rest of the epiblast is such that a triangular wedge of epiblast is left as the limit of the ganglionic formation. The point of this wedge, which exists in much the same form for a considerably later period of development, projects towards the mesoblast. It is somewhat difficult to describe these appearances in words; a glance at figs. 2, 14, 38 suffice, I think, to make clear the meaning of the Zwischenstrang of His, for that is what this portion of indifferent epiblast really is. Let us follow the lateral epiblast upwards from the side of the trunk to the lips of the neural plate. At first it is for some distance neuralwards only one layer thick; soon this changes, and it becomes gradually thicker; and if we follow it in such a section as is figured in figs. 14, 38, we see that at some little distance from the infolding neural plate it attains its maximum thickness (leaving the neural plate itself out of question as part of the epiblast). Beyond this point it abruptly becomes one-layered again, and remains one-layered till it ends also abruptly in the neural plate. The region of this one-layered epiblast is that from which the ganglionic Anlage has been cut out. The point of maximum thickness is that portion of epiblast which has just failed to take any share in the formation of the ganglion. This point was one which gave me a good deal of trouble in the course of the researches, but the explanation of it gave the key to the origin of the ganglionic Anlagen. In fact the first rudiments of the ganglia are formed from the deeper layers of the epiblast just outside the limits of the neural plate.

These stages in the formation of the spinal ganglia have never yet been seen or figured by any observer.

The involution of the neural plate now begins to take place very rapidly (fig. 15). Along with it the ganglionic Anlagen get carried upwards. It seems as though they had not time to get out of the way of the infolding process, and in missing the chance to get out before the involution begins they are bound, on account of pure mechanical processes—the explanation and description of which I leave over to others—to follow the neural plate, and thus they come to a somewhat abnormal position at and between the dorsal lips of the neural plate. The steps of this process are shown successively in figs. 14, 15, 5, 9, 21, 32.

Some figures of the head region (Nos. 38—42) are given under high magnification, and tell their own tale in justification of my statements of the very early appearance of the ganglia as epiblastic proliferations and their independence of the neural plate. They lie close to the latter, but can no more be regarded as outgrowths of it than any other two organs which lie close to each other in development can be considered, for that reason, as derivatives one of the other. I have nearly always been able, after the first traces of the ganglia were visible, to distinguish the lateral limits of the neural plate, and I think the reader will also have no difficulty in doing this in very many of the figures given in Pls. XVI, XVII, and XVIII.

In such figures as figs. 21, 33—36, 49, 50, 52, one sees that the lips of the neural plate are very sharply defined. This appearance was one which struck me as remarkable in the very beginning of the investigations, all the more as till now no observer seemed to have noticed it, and, so far as I am aware, there is only one figure of it in existence, pl. xvii, fig. 12, in Professor His's paper on the peripheral nervous system (No. 29). This figure also is taken from the spinal region of an Elasmobranch embryo, and tallies almost exactly with my figs. 22 and 32. Professor His, though he long ago noticed the appearance, incorrectly interpreted it, and attached no particular importance to it. I shall refer to it again in reviewing the work of previous observers.

To me it was the key to the origin of the ganglionic Anlage, for it showed me unmistakably that this Anlage was not, as all authors except His had supposed, an outgrowth of the spinal cord. The identification of this sharp line of division, however, was by no means a solution of the problem, for it was now a question of where the ganglionic Anlage really arises. The thin one-layered epiblast above the lips of the neural canal when contrasted with the many-layered epiblast in the region of His's Zwischenstrang, suggests at once a possible point of origin; but in Elasmobranchs at first no proof of this could be found, and so I had to look further back in earlier developmental stages before the neural plate is involuted. The results of this search are given above, and indeed it bears out my statement that this thin-layered epiblast above the neural lips is really the point from which the ganglionic Anlage has taken its origin. There is no need to demonstrate, by means of mathematical formulæ, &c., that the one-layered epiblast has during the involution of the neural plate undergone a good deal of tension,—a tension which no doubt helps to separate the ganglionic Anlage on each side from the epiblast.

We have now arrived at a stage such as is figured in figs.

32—36, 21, 13, 17, 43—45, where the Anlage of the ganglia sits upon and between the dorsal lips of the neural plate and prevents the closure and fusion of the latter.

The next step is the further proliferation and removal of the Anlagen to the sides of the spinal cord. In the words of most authors, we have now got to Marshall's neural ridge or crest, and the Anlagen "begin to grow out of the spinal cord" (Marshall, Nos. 45, 46).

I think that in the preceding lines I have shown clearly enough that there is really no outgrowth from the spinal cord, nor do I find myself in the position to support Marshall's view of the origin of the ganglia from a neural ridge. From the time of their first formation the ganglionic Anlagen appear to me to be segmented, and if the Anlage of one segment passes over into that of another in this and some of the following stages, I can see in this no reason for saying that the spinal ganglia arise from an unsegmented ridge of cells. No one attaches great morphological importance to the origin of the muscle-somites from an apparently unsegmented structure, an origin which is conditioned by the mode of formation of the cell elements, and as all traces of such a continuous structure soon disappear, the whole of its elements passing over into the various spinal ganglia without leaving any permanent "commissure," I must hold that if we are to say that the spinal ganglia are outgrowths of a neural ridge, we must not forget two things: that the outgrowths begin as epiblastic buds long before the neural ridge stage; and secondly, that the whole of the neural ridge is absorbed by the various spinal ganglia. This latter point is all the more necessary seeing that at least one observer has suggested as an hypothesis worthy of proof the origin of the lateral nerve of fishes from the remains of the neural ridge. M. Julin says (No. 39, p. 31), "Dans mon idée le nerf latéral, tel qu'il se trouve constitué chez l'Ammocoetes ne serait que le reste de la crête neurale, ce qui expliquerait ses rapports avec les racines du vague et les branches dorsales des nerfs spinaux dorsaux." He is further of opinion that this avowed hypothesis "méritерait d'être soumise à un contrôle rigoureux, par des recherches embryogéniques." In face of the known facts concerning the morphology of the lateral nerve as detected by van Wijhe and myself, we may regard with perfect indifference M. Julin's researches in the direction of the above hypothesis. Such researches will turn out to be neither more nor less than a wild-goose chase.

In my statements that the whole of the so-called "neural ridge" passes over into the ganglionic formations, I agree completely with Sagemehl, Onodi, and His. Balfour and Marshall held different opinions which now can no longer be maintained.

The ganglionic Anlage—now that it lies on the lips of the neural plate, seems often to possess an unpaired character, but from its subsequent fate, and from the appearances presented in such figures as my figs. 21 and 29, it must really be considered as a paired structure, a point of the truth of which the lateral origin of the Anlagen is sufficient evidence. The Anlagen now begin to grow out from their position above and between the lips of the neural plate (figs. 22, 23, 33—36), and wander to their permanent position at the lateral portion of the spinal cord (figs. 8 and 30).

We are now treading on ground which has been fairly worked, but there are none the less one or two points of extreme importance to which a few words must be devoted. As we have seen, until now the ganglionic Anlagen have really no attachment to the spinal cord; and during the growth downwards to its lateral side they are, as Sagemehl (No. 56, p. 30) first showed, quite independent of that structure (fig. 57). The difference between Sagemehl's account and my own is obvious when we remember that he, along with most other observers, regarded the ganglia as outgrowths of the spinal cord. I maintain—and the figures prove the truth of my view—that neither now nor before are the ganglia attached to the spinal cord. The first and only attachment to the spinal cord is the permanent one now soon to be acquired. Before the attachment takes place the ganglionic Anlage of each side divides into two portions, the definite spinal ganglion and the sympathetic ganglion (fig. 59). The latter will not concern us here, though on this system of ganglia I shall later on have more to say. The development of the sympathetic has been worked by Balfour (Nos. 1 and 2), and more fully by Onodi (No. 52).

Arrived at the lateral surface of the spinal cord (figs. 28, 31, 61) the attachment[1] to the latter takes place. On this point, which in my opinion it is difficult to decide for the spinal ganglia by direct observation, differences of view also obtain. Sagemehl (No. 56, p. 31) and others hold that the connecting fibres grow out from the spinal cord, while Professor His (No. 34, p. 373), with great confidence, says, "Die sensibeln Nerven, der N. acusticus, und die Geschmacksnerven entspringen in dem Ganglion und sie wachsen mit ihren centralen Wurzeln in das Rückenmark und in das Gehirn herein. Diesen Satz, den ich früher nur indirect zu stützen vermöcht hatte, vermag ich nun mit grosser Sicherheit zu beweisen."

His was the first to apply the physiological laws of the trophic properties of the ganglia to the solution of this question. He says (No. 29, p. 477), "Die Frage, ob die hinteren Wurzeln vom Rückenmark aus nach den Ganglien hin wachsen, oder von den Ganglien aus nach dem Rückenmark, ist bis jetzt noch ziemlich unerörtet geblieben. In meinem Augen spricht das Uebergewicht der Gründe für die letztere Alternative. Als einen dieser Gründe betrachte ich die durch Waller und durch Cl. Bernard (No. 12) nachgewiesene Trophische Abhängigkeit der hinteren Wurzeln vom Ganglion. Bei Durchschneidung der hinteren Wurzeln zwischen Rückenmark und Ganglion degenerirt nach den Ergebnissen jener Forscher der mit dem Rückenmark in Verbindung stehende Stumpf; der mit dem Ganglion verbundene bleibt intakt (No. 12, Bd. I, p. 237). Jede Zelle eines Ganglions nimmt nämlich zunächst eine spindelförmige Gestalt an, dann aber wächst sie in zwei Fasern aus, die nach entgegen-gesetzten

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[1] Marshall (Nos. 46, 49) held this to be a secondary attachment. It is the first and only connection with the central organ.

Richtungen vom Zellkörper abgehen, &c." I am inclined, and was so before reading these words, to agree with Professor His in his conclusions that the growth is a centripetal one; indeed, as Dr. Hill ('Three Lectures,' p. 3, No. 27) also has insisted, the matter is one of which the physiologists have already furnished the solution. He says, "It appears probable that the fibres of the posterior roots also grow from the cells of the ganglion centralwards into the cord, instead of from the cord to the ganglion as usually supposed. A consideration of the effects of cutting nerves in such cases as have been hitherto described leads me to formulate the law that nerve-fibres die when cut off from the cells of which they are processes, and from which they derive their nutrient supply. It is well known that, when the posterior roots are cut, the fibres which remain attached to the root-ganglia live; those entering the cord die."

I will not cast any doubt on Professor His's very positive statements on this point, indeed, I believe they represent the facts of the case, but I must again say that the question is difficult, if not impossible, to decide for the spinal ganglia by direct observation, and for myself, I must admit that I have not been able to make more of it as yet.[1]

The mode in which the connection between the ganglia and their peripheral end organs takes place, is one on which there is also much dispute. For His (No. 33, p. 375) and Kölliker (Nos. 42, 44) hold, as against all other observers, that the nerves are processes of the ganglionic cells, without any intervention of ganglionic cells or ganglionic cell nuclei in the course of the nerve. I shall have occasion to discuss this question more fully in connection with the anterior roots of spinal and cranial nerves, and content myself here with the remark that I believe Professor His's and Kölliker's conclusions cannot be maintained, and that the peripheral connection in the case of sensory or

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[1] As an absolute maxim I am only inclined to support this as regards the spinal ganglia; in the case of the cranial ganglia, as we shall see, there are reasons for holding this view only with regard to the sensory part of the root.

motor nerves is brought about rather by a chain of ganglionic cells.

I, *b*. THE CRANIAL GANGLIA IN ELASMOBRANCHII.

Compared with the development of the cranial ganglia that of the spinal ganglia previously described is simplicity itself. For just as the head of Vertebrates presents, when compared with the trunk, a complexity of problems, the solution of which, in the opinion of morphologists like Huxley, Dohrn, Froriep, and others, will take years of careful work, so also the cranial ganglia present a number of problems, towards the solution of which I only can hope to go a little way in the following pages.

While there can be no sort of doubt that the spinal ganglia are strictly segmental in their origin—indeed, that such is the case is easily demonstrable—the reduction of the cranial ganglia to segmental order is a task of great difficulty. It has been objected by Dohrn and others that the setting up of tables showing the segmental nature of the head nerves is a proceeding which is to be deprecated, and that the true problem is the reduction of the components of the head to simpler Annelidan structures. To which one may reply that, according to Dohrn, such Annelid ancestors were segmented animals, and no matter how complex the Vertebrate head may now be, it is at its basis composed of a number of Annelid metameres, and the unravelling and ordering of the existing complex, as far as it is possible, is the real task of the morphologist.

I shall not at the moment attempt to discuss again the claims of the various cranial nerves to "segmental rank," a proceeding which, to my mind, is entirely justifiable, for it has its meaning in the sorting of the cranial nerves for morphological (and physiological) considerations. Still, in the following account of the very first signs of the cranial ganglia, I must insist on such points of development as support, for instance, the comparison of the auditory and olfactory ganglia and sense organs with those of, for example, such a typical cranial nerve, its ganglion, &c., as the glossopharyngeus. This is all the more in place, as Professor His, in his recent note of warning against the speculations of us unfortunate younger morphologists, does not hesitate to maintain as a fact the derivation of the auditory and olfactory organs from what he calls the "ganglion Leiste," which also gives origin to such ganglia as facial, glossopharyngeus, &c. I hope to show to Professor His's satisfaction that this "fact" is as little a fact as his derivation of the spinal ganglia from the "Zwischenstrang," which is the continuation backwards of the "ganglion Leiste" of the head.

A further complication is presented by the superaddition of the sense organs of the head (and their ganglia), excepting the eye, which all enter into relationships with those portions of the head ganglia which appear morphologically to correspond to the spinal ganglia. These complications will be more clearly explained in the course of the work.

I have mentioned in a recent paper (No. 8) that the cranial ganglia are made up of more form elements than the spinal, and I observe that Professor Gegenbaur, without investigating the development, comes to the same conclusion (No. 21).

The first traces of the cranial ganglia Anlagen are formed in exactly the same fashion as those of the spinal ganglia, and it is much easier, on account of their greater distinctness, to make out the earliest stages. In the embryo in which I described the first traces of the spinal ganglia such Anlagen can also be distinguished in the head region. As the mesoblast has not yet divided up into the body-somites, or so-called protovertebræ, the head-somites are also not formed, and so we are entitled to say generally, the traces of the posterior root ganglia of cranial and spinal nerves are formed very early and long before the closure of the neural plate.

A figure through the head region of an embryo, as early as the one depicted in fig. 4, has been given by Professor Marshall in one of his papers (No. 48, fig. 1), but he gave no trace of any ganglionic formation, and, indeed, it is quite possible that such traces were not differentiated in the section from which he figured. In his monograph of the development of Elasmobranch fishes, Balfour has also given, on Pl. IX, many figures of stages corresponding to those on my Pl. XVI; but here again no trace of the ganglionic Anlage, which is seen in all my figures, has been represented.

In fact, of the cranial, just as of the spinal ganglia, no observer has hitherto seen the very first stages which I am about to describe, and the last observer, Onodi (No. 51), who has given no figures at all, has, judging from his description, only seen the Anlagen in much later stages, and, as we shall afterwards see, has not interpreted rightly or seen all that is to be seen in fairly decent sections.

Returning to fig. 4, we find, on examination, the same appearances (*g. a.*) as were met with in the developing spinal ganglion. If we examined an earlier stage than this we should meet with no trace of the Anlagen of the cranial ganglia. We see now a central portion which represents the brain part of the neural plate in section. At each side of this, but independent of it, one notices the budding out and separation, so far as the lateral epiblast is concerned, of a process which is, as we shall see, the first trace of a cranial ganglion, or rather of part of one. Soon after this phase the involution of the neural plate begins just as in the case of the spinal cord, and along with the involution the ganglionic Anlagen are also carried upwards. I have figured these stages in figs. 6, 10—12, 16, 19, 20, 39—43, taken from various parts of the brain, in order to show that this mode of development holds for portions of the olfactory ganglion (figs. 19, 20), mesocephalic or ganglion of the ophthalmicus profundus (No. 7), trigeminus, facialis, auditory, glossopharyngeus, and vagus.

The involution of the neural plate, on its completion, encloses the cranial ganglionic Anlage just as occurs in the spinal cord. A number of figures of this stage are given in figs. 18, 21, 24, 25, 29, 45, 48, *g. a.*

The Anlage is now separated from the skin, and in the head of Elasmobranchs no trace of a Zwischenstrang is left behind.

If in such stages it is difficult in the trunk to be always quite certain of the sharp boundary line separating the ganglionic Anlagen from the closing neural plate, such is never the case in the head. I cannot remember having seen a single Elasmobranch section in which for the head it was at all a difficult matter to distinguish the limits of the two; and in spite of this fact there are no figures in existence which show this separation such as I depict it in figs. 44—48, 24—27, 29. Here, as in the trunk, the position of the ganglionic Anlagen between the lips of the neural tube (figs. 25, 44, 47) prevents their complete closure. But soon the Anlagen begins to grow downwards and outwards towards the lateral surface of the body. This outward growth leads, as is well known from the researches of recent years, to a difference in position between the ganglia of the head and those of the trunk. For while the latter lie between the muscle-plates and the spinal cord, the former take up a position outside the mesoblast and close to the skin.

The portion of the ganglionic Anlagen of the head derived from the neural epiblast corresponds, in development at least, with the Anlagen of the spinal ganglia, but the cranial ganglia of (apparently) all Vertebrates acquire a further form-element derived from the lateral epiblast above the gill-clefts, and at about the level of the notochord. For the formation of this element I have not in this paper given any figures, but I think such figures can be here entirely dispensed with, seeing that in a former paper (No. 6) treating of the branchial sense organs and their ganglia I figured a great many stages of this ganglionic formation, for, what I there called the branchial ganglia make up this additional form-element of which I just wrote. I believe I showed conclusively enough in that paper that above the gill-cleft ganglionic elements were given off into the main ganglion—indeed, it then seemed to me that most, if not all, the ganglion was formed there. As even such a severe critic as Professor Gegenbaur expresses himself satisfied that such form-elements of the ganglion take their origin above the gill-cleft, I may assume it to be unnecessary to give a very detailed account of such formation in individual cases. From Professor Gegenbaur one must apparently be thankful for small mercies, and as this is the one thing in my researches which he admits unreservedly that I have seen, I quote his testimony in my favour. He says (No. 21, p. 41), "Die Beziehung des Ganglions zu dem Ektoderm ist von Beard richtig erkannt worden : er sagt, 'The proliferated cells form a mass of actively dividing elements still connected with the skin and fused with the dorsal root; . . . . . for some time the cells continue to be given off, and of those already given off many show nuclear figures.' Die epitheliale Verdickung hat also die Bedeutung einer Quelle der Ganglienbildung. Das geht auch aus den bezüglichen Figuren Beard's hervor, die zudem in der Anordnung der Elemente der am Ganglion befindlichen Ektodermschichte gar nichts aufweisen, was man auf ein hier sich bildendes Sinnesorgan beziehen könnte. Wenn die Thatsachen, wie sie in Wirklichkeit bestehen, die Grundlage der Forschung abgeben, so kann man hier nur sagen; der Nerv wächst vom Centralorgane aus unter dem Ektoderm bis zu einer Stelle, an der ihm aus dem Ektoderm ein Zufluss von Formelementen zu Theil wird."

For the present moment I leave entirely alone Professor Gegenbaur's doubts about the sense organs. Such doubts are entirely unjustifiable. To return to the ganglionic Anlagen derived from the epiblast at the neural side of the head. These Anlagen grow outwards and downwards towards the lateral surface of the body. Just above the gill-cleft there is here a small portion of neuro-epithelium (figs. 94, 95), which is the Anlage of the branchial sense organs or lateral sense organs. This neuro-epithelium has begun to extend its growth before the ganglionic Anlage fuses with it.[1] In figs. 94, *a* and 95, *a*, I have represented this. The growth has

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[1] Fig. 101 shows this growth for the auditory epithelium of a lizard. Just as all the lateral sense-organs are formed from a certain limited number of pieces of neuro-epithelium, so all the sensory cells of the ear arise from the extension of one little bit of neuro-epithelium (*o. e.*)

already extended behind the gill-cleft (fig. 95, *b*), and also in front of the gill-cleft (fig. 94, *a*). In connection with the morphology of nose and ear this point is one of considerable importance, and I shall have occasion to refer to it again. The ganglionic Anlage now fuses with neuro-epithelium at one point. At the point of fusion a proliferation of the cells of the neuro-epithelium takes place into the ganglionic Anlage. The proliferated cells form a mass of actively dividing elements still connected with the skin, and fused with the rest of the ganglionic Anlage. Externally to this thickening is situate what Professor Froriep (No. 17) and I regard as the primitive branchial sense organ of this segment. Here again I refrain from discussing any of the questions connected with the formation and morphology of these sense organs.

One fact at least holds as the result of this skin fusion, and this is that a number of form-elements are given off into the ganglion. The recognition of this fact does not come to me after reading Professor Gegenbaur's paper quoted above. I had long before seeing that written as a note, on p. 21 of my paper (No. 8), on the "Old Mouth and the New," "The cranial ganglia of Vertebrates are far more complicated morphologically than has hitherto been recognised. In addition to parts which appear to correspond morphologically to the posterior root ganglia of the spinal nerves plus the sympathetic ganglia, they also contain the special ganglia which are formed in connection with the gill sense organs."

The ganglion complex soon begins to leave the skin, and in doing so a number of cellular fibrous cords are left behind connecting the sensory epithelium with the ganglion complex.

The sensory epithelium has, briefly stated, usually grown in three directions in front of the gill-cleft, behind the gill-cleft, and above the gill-cleft, either in a neural, or a forward, or a backward direction. The nerves connecting these various sensory elements with the ganglion appear to me to be all derived as splittings off from the inner layer of the sensory epithelium. This view, which I formerly only mentioned as true for the suprabranchial nerves, I must now also extend to the præbranchial and the sensory part of each postbranchial nerve.

The ganglion complex has also to acquire its first and permanent connection with the central nervous system, and of the mode in which this takes place there can be no sort of doubt. The main trunk of the nerve and its connection with the central nervous system are formed respectively by the formation of nerve-chains from some of the ganglion-cells, and by the growth of fibres into the central nervous system.

Here again, however, the cranial ganglia present us with complications as compared with the spinal.

It is well known that the whole of the motor fibres of the spinal nerves (those to the voluntary and the visceral muscles derived respectively from the anterior and lateral horns) pass out in the anterior roots. Now, there can be no doubt that the whole of the anterior root of a spinal nerve is a direct outgrowth from the central nervous system. All observers are agreed on this point. Quite other conditions obtain in the head. In the oculomotorius, trochlearis, and abducens, the only nerves which are comparable at all to anterior roots of spinal nerves, no fibres are derived from the homologue in the head of the lateral horn of the spinal cord; in other words, the anterior roots of the head give no fibres to visceral muscles, and—a fact which is well known—the fibres to the visceral muscles of the head pass out with the posterior roots of the cranial nerves. It appears also that these fibres take their origin in the continuation of the lateral horn in the head. This being so, and it being also true that all other motor nerves, including those of the spinal cord and the three eye-muscle nerves, certainly occur as outgrowths of ganglia[1] situated within the central nervous system, it becomes a question whether the motor fibres of the gill-cleft muscles are not also direct outgrowths of the central nervous system. I must confess that I have not as yet been able to settle this point by

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[1] See fig. 100, which depicts the third and its central ganglionic origin as seen in *Lacerta agilis*.

direct observation, but I do not hesitate for a moment in expressing the opinion that such is the case. If this be true it follows that a typical posterior root of a cranial nerve, that is, a root passing to a gill-cleft, is composed of elements derived from at least three sources: there is, firstly, the portion which corresponds to the true spinal ganglion[1] in its derivation from the epiblast just outside the neural plate (neural ganglion); secondly, a portion formed in connection with the branchial sense organs (lateral ganglion); and thirdly, a portion derived from the continuation of the lateral column in the head.

In addition, a part must be added comparable to the sympathetic ganglia of the trunk, and this portion is probably, as occurs in the case of spinal ganglia, contained in the portion of the ganglion derived from the epiblast, just outside the neural plate.

Here we are faced by some interesting problems, which I will afterwards discuss.

His (No. 34, p. 394) and others have raised objections to the view of Balfour, that the cells derived from the neural ridge or crust are the Anlage of the posterior roots of the cranial nerves. Balfour's phraseology has been used by Marshall, Spencer, van Wijhe, myself, and others. No doubt objections may be urged against the use of this phraseology as accurately representing all the facts.

While I admit that these cells are more a ganglionic Anlage than that of a nerve, there are two points which must be urged in extenuation of the offence, if offence it be. In the first place, Balfour, Marshall, van Wijhe, and all of us who have used this phraseology, have done so, in the sense of the inclusion in the term posterior root, both root and ganglion of the nerve; and secondly, in the head at any rate, in addition to the cell processes which grow from the ganglion into the central organ, it can be demonstrated (fig. 103) that some of the cells of the ganglionic Anlage pass over into the root of the nerve, and take a direct share in its formation. This question

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[1] This portion of the cranial ganglion is possibly only morphologically an equivalent to the sympathetic part of a spinal ganglion.

of the formation of nerves is one on which, along with most observers, I am completely at variance with His (Nos. 29 and 34) and Kölliker[1] (Nos. 42 and 44); and I refer the reader to a fuller discussion of it in another part of this paper.

With this I close my account of the very earliest stages of the cranial ganglia in Elasmobranchii. The mode of development here described from at least two sources is characteristic for the ganglia of all the branchial nerves, facial, glossopharyngeus and vagus (fig. 24), and also for the trigeminus. Mutatis mutandis it also holds for the olfactory (figs. 19, 20), mesocephalic, and auditory (figs. 25, 29) ganglia. Here I will only emphasize this point, reserving to myself the right to return to it on a subsequent occasion. To go further into the matter here would lead to the discussion of a great many disputed points, and for the moment I wish to lay more stress on the absolute facts of the development which can be demonstrated. The conclusions which I feel entitled to draw from those facts can for the moment be postponed.

II. The Peripheral Nervous System of the Chick.

Our knowledge of the development of the peripheral nervous system in Birds is almost entirely due to His (No. 29), Marshall (No. 46), and Onodi (No. 51). Kastschenko (No. 40) has also contributed his item, which, so far as nerves or ganglia are concerned, is of no particular value, for it contains no new facts and throws no new light on the morphology of either cranial or spinal nerves and ganglia.

For many reasons I was obliged to include the Chick in the sphere of my observations. For one thing His's remarkable observations and hypotheses were mainly established for this animal (Nos. 28, 31), and I could not feel satisfied until the explanation of His's Zwischenstrang was got at the bottom of. The striking manner in which the epiblastic origin of the

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[1] Kölliker has upheld his views in several papers.

ganglia in the head of the Chick attracts the attention in good sections was also a reason for fully investigating the development in this animal; for the question naturally arises, Are these appearances primitive, or is the development modified in some way or other in the Chick? One could hardly hope to maintain, as a strict morphologist would be almost bound to do, if he had only Onodi's researches to go upon, that the mode of development of the cranial ganglia in the Chick is a more primitive one than that in Sharks. The facts, which I had discovered before seeing Onodi's paper, were at first a great puzzle to me, a puzzle to which Onodi's researches have given no solution; for, according to him, and so far he agrees with Marshall (No. 46), the cranial ganglia of the Chick differ entirely in mode of development from the ganglia, cranial and spinal, of all the other forms, Sharks, Lizards, Mammals, &c., which he had examined. Indeed, he maintains—and I find this attitude a surprising one in the man who had seen the true development in the cranial ganglia of the Chick—he maintains that in all other cases the ganglia, both cranial and spinal, are developed as outgrowths of a ganglion ridge (neural ridge of Marshall), and this in its turn owes its origin to the central nervous system.

Seeing that my researches on the cranial ganglia of the Chick are partly a confirmation of Onodi's, it might be supposed that there was no necessity for giving them in detail. However, I am of a different opinion, for they do not agree with Onodi's results on all points, and on the fundamental question whether the ganglionic Anlagen of the head are or are not parts of the central nervous system, Onodi says nothing. As he holds that in all other cases the ganglia, spinal and cranial, are outgrowths of the central nervous system, his position as a comparative embryologist is not a very logical one. The first traces of the ganglia, both cranial and spinal, are met with in the Chick between the twenty-second and twenty-sixth hours of incubation. In such embryos there are on the average from two to ten body-somites or protovertebræ, and it is in such embryos that evidence of the epiblastic origin of both cranial and spinal ganglia can nearly always be obtained.

The mode of preparation, which in Sharks is not of such importance, is here a very weighty factor. My embryos were all prepared by immersion for from half an hour to two hours in Flemming's chromic-osmic-acetic acid mixture, and afterwards stained with borax carmine or picro-borax carmine. Osmic acid must be used here, and used very carefully, or otherwise no guarantee can be given that all the appearances depicted by me in Plates XIX, XX, XXI will be visible. Thin sections are of course also of importance, and I must express the opinion that the results obtained by Professor His ten years ago (No. 29) are vitiated by improper treatment of the embryos and by the thickness—at that time unavoidable—of the sections. My sections are mostly $\frac{1}{200}$ mm. thick. As was the case in the account of Elasmobranchs, I shall begin this part of the paper also with the

II, *a*. DEVELOPMENT OF THE SPINAL GANGLIA IN THE CHICK.

The appearances about to be described may be even seen sometimes in embryos in which no body-somites are as yet formed, and, speaking generally, an embryo with about six body-somites will show in different regions the appearances presented in seven sections (figs. 70—76) taken from the spinal region of such an embryo with six mesoblastic somites. It will be noticed that the medullary canal is everywhere open, and, in fact, here, as in Sharks, the first traces of the cranial and spinal ganglia are formed long before the closure of the neural plate. The first section is in the region of the primitive streak—and here no trace of ganglionic Anlagen is to be seen (fig. 70). The next section (fig. 71) is taken much farther forwards, and on the left side of the section, at any rate, the commencement of the ganglionic differentiation (fig. 72, *g. a.*) can be seen. The third section (fig 72) passes through the middle of a mesoblastic somite on the right—and here it is difficult to distinguish a ganglionic Anlage—but on the left it has cut the segment near its end and the ganglionic Anlagen is distinctly seen at *g. a.* as a small plug of cells being cut out of the epiblast just outside of the neural plate.

The fourth section (fig. 73) shows very distinctly on both side the spinal ganglionic Anlagen (*g. a.*). The boundaries of the infolding spinal cord are sharply marked off at *o* from the ganglionic Anlagen, which lies just outside them at *g. a.* This figure shows that the spinal ganglia in the Chick take their origin in exactly the same way as those of Elasmobranchii, and that by the cutting out of the ganglionic Anlagen at *g.* the epiblast to the outer sides of them is left as a somewhat triangular body, which, as in Sharks, where it is not so distinct, represents the "Zwischenstrang" of His. The following three figures, taken still farther forwards from the embryo, show the same appearances even better. On examining, for example, the six figures (fig. 75, 76, 80, 81, 85, 89), one sees the following things:—The spinal cord is rapidly closing in, and its lips are sharply defined from the ganglionic Anlagen (*g. a.*) just outside them. With the lateral epiblast (*e.*) the Anlagen of the ganglia have lost all connection, and only retain it with the epiblast at the re-entering angle between spinal cord and skin. The epiblast at *ie*, of which the Anlagen, as in figs. 70, 71, originally formed a part, is, ever since the separation, only composed of a single layer of cells, which, in consequence of the tensions arising in connection with the infolding process, has become much lengthened. Outside this thin-layered part the epiblast passes almost abruptly into a much thicker-layered portion of the outer layer, which has taken no share at all in the formation of the ganglia. This thicker portion (fig. 68) forms a somewhat triangular mass of cells, the apex of which is directed towards the mesoblast. From a consideration of these figures (figs. 75, 76, 80, 81, 85, 89,), and of several other figures (figs. 98, 99, 102), to be afterwards noticed more in detail, the conclusion is forced upon any unbiassed observer that the triangular mass of cells is identical with the so-called "Zwischenstrang" of His. The consequences of this conclusion are fatal to the observations which His recorded nearly ten years ago, and to which he has been true for nearly twenty years.

The next stages in the formation of the spinal ganglia which we need consider are represented in Pls. XVIII, XIX, and XX, figs. 51, 55, 98, 99.

The separation of the neural tube from the epiblast has now taken place, and the ganglionic Anlagen have also no longer any connection with the epiblast. The spinal cord has not yet really closed, for its lips have not met, and in all the figures they are sharply defined from the fused ganglionic Anlagen which lie between and above them. In all the figures, but especially in 55, 98, 99, the Zwischenstrang of His (*z.*) is a prominent object. It is represented under very high power in figs. 98 and 99. As in Elasmobranchs, the ganglionic Anlagen now begin to grow down the sides of the cord, leaving their position above the lips of the neural tube; a stage of this process, showing that they are still unconnected with the cord, is given in fig. 102. When the Anlagen leave the lips of the neural tube the latter close together, and all subsequent stages go on exactly as described in Elasmobranchs. As I can here record no new facts I leave the development of the spinal ganglia of the Chick at this stage. I have proved at least three things for the spinal ganglia of the Chick. (1) That they are direct epiblastic proliferations formed very early outside the limits of the spinal cord Anlagen; (2) that there is no outgrowth of cells from the spinal cord to form them; (3) that the Zwischenstrang of His is that part of the epiblast which just fails to play any part in the formation of the ganglia. A fourth conclusion may be drawn, and this also holds for Elasmobranchs and other forms. It is that there is no form element in the spinal ganglia corresponding to that portion of the cranial ganglia which is derived from the sensory epithelium of lateral sense organs.

II, *b*. THE CRANIAL GANGLIA IN THE CHICK.

As we have seen, the development of the cranial ganglia in the Chick was described by Marshall (No. 46) just ten years ago. He says, p. 15, "About the twenty-second hour a small outgrowth of cells appears along the mid-brain on each side, at the angle between the external epiblast and the neural canal—the neural ridge. This rapidly extends both forwards and backwards; forwards as far as the anterior part of the optic vesicles; backwards, along the whole length of the brain, and a certain distance down the spinal cord. Its first appearance precedes the closure of the neural canal." And on p. 12 (1), "The neural ridge appears before closure of the neural canal is effected, so that the ridges of the two sides are primitively independent of each other." (2) "The ridge is not developed directly from the external epiblast or from the neural canal, but from the re-entering angle between the two."

His (No. 29) has also given some partially correct figures of the first origin of the cranial ganglia in the Chick (Taf. xvii, fig. 3, *a*—*f*). The remaining figures of the series *g* and *h* are, I think, not correct; and the interpretation put on the (only partially correct) figures by His is one which, along with Balfour, I cannot accept.

His himself (No. 29, pp. 464—465) summarises his conclusions as follows:

"Ich halte dafür, dass das Gebilde, welches ich beim Hühnchen Zwischenstrang genannt habe, weder eine 'Wucherung' des Medullarrohres, noch einer solchen des Hornblattes seinen Ursprung verdankt, sondern einem zwischen diesen gelegenen besonderen Substanzstreifen. Dieser Substanzstreifen grenzt sich schon vor Eintritt des Markschlusses in mehr oder minder auffälliger Weise ab und so bildet er eine Rinne, die von mir sogen. Zwischenrinne.

"Nach meiner Ansicht gliedert sich demnach das obere Grenzblatt oder Ectoderm in dreierlei Anlagen; in die Medullarplatte, in die beiden Zwischenstrang-platten und in das Hornblatt. Nach vollendetem Rückenschluss ist auch die Zwischenstrang-Anlage *vom Hornblatt überdeckt*,[1] ihre Stellung aber zur Medullardecke wechselt in den verschiedenen Bezirken, indem sie in dem einen über, in den anderen neben dieselben zu liegen kommt.

"Beistehende schematisirte Abbildung, in welcher die Zwischenstrang-masse weiss ausgespart ist, kann die Art des Zustandekommens veranschaulichen. Es nimmt nämlich der abgelöste Zwischenstrang beim Hühnchen nur am Kopfe und zum Theil nur über dem Vorderhein und dem Mittelhirn die intermediäre Stellung zwischen Medullarrohr und Hornblatte ein, weiter hinten bildet er, so weit er nicht zu Anlage der Gehör-grube verwendet wird, zwei seitlich von der Schluss-stelle liegende, auf dem Durchschnitt dreikantig erscheinende Leisten. Von diesen letzteren haben Balfour, Marshall, und Kölliker referirt, ich sehe sie als 'Auswüchse' oder als 'Wucherungen' des Hornblattes an, eine Ansicht, die ich in keiner Weise vertrete (!). Für mich fängt das Hornblatt erst da an, wo die Ganglienanlage aufhört, und die Ganglienanlage da, wo das Medullarrohr aufhört; ich verwerfe überdies, wie ich schon an anderem Orte ansgesprochen habe (Briefe über unsere Korperform, S. 67, u. f.) das von Manchen Embryologen so freigebig benutzte Princip der lokalen Wucherungen."

My account of the cranial ganglia of the Chick is in most points in agreement with that given by Onodi (No. 51, p. 260), to whom the reader may refer for a fuller account. In a later paper (No. 52) Onodi himself describes his results in the Chick briefly as follows (p. 553):—"Beim Huhn stammt das Ganglion intervertebrale[2] am Kopfe theils von der Zellenproliferation, theils von der gleichseitigen Abschnürung des der

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[1] The italics are mine.

[2] When, as here and elsewhere in his papers on nerve development, Onodi speaks of the cranial ganglia as "spinal ganglia of the head," he is begging entirely the question of the homology of the two sets of ganglia. There is no discussion of the homology in any of his papers (see list at end of this work), neither do his researches contain any facts which justify this baseless assumption of their homology.

Umbiegungsstelle in das Gehirnrohr naheliegenden Abschnittes des Ectoderma."

As in Elasmobranchs the first traces of the cranial ganglia Anlagen in the Chick are found in embryos in which as yet no division of the mesoblast has taken place. Marshall's statement of the time of first appearance, viz. the twenty-second hour, may be taken to be as nearly correct as one can determine.

The neural tube is still quite widely open.

Figs. 86, 87, and 67 are sections through the head region of three such embryos. In fig. 86 no trace of the ganglion Anlagen is to be seen, but the epiblast is much thickened, especially in the region of the future central nervous system and ganglionic Anlagen.

In fig. 87 traces may be seen of the ganglionic Anlagen at *g. a.*, and one sees that they occupy practically the same position in reference to the central nervous system as the spinal ganglion Anlagen. In figs. 82, 83, and 84 are figured three sections through different regions of the head of a Chick embryo with seven body-somites. In all these sections the origin of the ganglia is very easily distinguishable. In fig. 82, which is through the region of the fore-brain, the limits of the neural plate are already marked out, and outside this the ganglionic Anlagen of each side are visible as special differentiations of the epiblast of the re-entering angle between the neural canal and the external epiblast, and also of a portion of the lateral epiblast beyond this. One notices that here, as in the spinal cord, the separation of the ganglionic Anlagen will cut out a particular region of the inner epiblast, and will leave a structure at *Z.* which is comparable to, and, indeed, identical with, the Zwischenstrang of His in the region of the spinal cord. Fig. 83 is in the region of the mid-brain, while fig. 84 is taken farther back from the hind-brain; these two sections present exactly the same appearances, and in a more marked degree than fig. 82. Figs. 77—81 are taken through the hinder head region of a Chick embryo with nine body-somites or so-called protovertebræ. Here the development of the ganglia has advanced a step farther. The boundaries of the central nervous system are well marked in all the sections, and one can see that the latter is not connected with the ganglionic Anlagen. In this series of figures, which go backwards to the hind-brain, the ganglia Anlagen are already separated from the epiblast outside the re-entering angle between brain and epiblast, but still connected with the epiblast of the re-entering angle. For Professor His's satisfaction it may be added that in all the sections a Zwischenstrang is more or less developed. The next stages are shown in figs. 97, 46, 63, 65, 66, which are taken through embryos with, on the average, eight to ten mesoblast somites. The central nervous system with the ganglionic Anlagen are now shut off from the outside by the meeting and fusion of the external epiblast.

The lips of the neural tube itself have not yet closed, because the ganglionic Anlagan, which in some of the figures (figs. 97, 88, 46) have still a distinctly bilateral character, still exist between and above them. The ganglionic Anlagen soon become entirely separated from the epiblast, and in doing this leave behind them the traces of the limits of their epiblastic origin in the shape of a three-cornered ridge of cells which is identical with His's "Zwischenstrang"[1] of the spinal region. It is figured at *Z.* in figs. 88 and 89. By the growth outwards from their position above and between the lips of the neural canal, the latter is able to close, and does so without having contributed a single cell to the formation of the ganglia.

The ganglionic Anlagen now begin to grow downwards towards the lateral surface of the brain to the point at which they acquire their permanent and only roots of attachment. The attachment takes place as in Elasmobranchs, and what I said about these forms on this subject may be taken as holding for the Chick also.

On the other hand, a portion of the "Anlagen" grows towards the lateral epiblast at about the level of the noto-

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[1] There is no such structure in the head of the Chick or any other Vertebrate I have as yet examined as His's Zwischenrinne.

chord and fuses with it (figs. 90, 91, 92, 93). I have not seen any reason for giving numerous figures of this point; those represented appear to me sufficient for the purpose. We are now concerned with the rudiments of the branchial sense organs. These structures were first described for Mammals by Professor Froriep (No. 17), and very shortly after his discovery my own preliminary researches independently announcing almost the same facts for Elasmobranchs appeared (No. 5). In the full account I afterwards gave of them I also mentioned the finding of similar rudiments in three-days-Chick embryos (figs. 90, 91, 92, 93). Béraneck (No. 10) afterwards confirmed the discovery, and Kastschenko (No. 40) in the account he more recently gave of them, with his characteristic failing, conveniently forgot to mention that either Béraneck or I had ever seen the structures which he described.[1]

However, the following conclusions regarding the importance of the rudimentary branchial sense organs for the embryo Chick are peculiarly my own.

We saw that in Elasmobranchii the fusion of the ganglionic Anlagen with the neuro-epithelium which forms the Anlagen of the branchial sense organs leads to a certain amount of ganglion form-elements passing from the neuro-epithelium to the main ganglion. Such portion is really the ganglion of the branchial sense organs or sense organs of the lateral line (figs. 92, 93) (lateral ganglion).

It can be demonstrated also for the Chick that such form-elements pass by proliferation from the rudimentary sense organ into the ganglion (figs. 92, 93). This being so, and it being also capable of demonstration that the sense organs, with

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[1] As Herr Kastschenko quotes my paper, I presume he was aware of the discovery; this conclusion is all the more justified as Professor Wiedersheim also briefly mentions my discovery in the last edition of his 'Lehrbuch der Vergleichenden Anatomie der Wirbelthiere' (p. 332). Professor Strasser also recently accuses Herr Kastschenko of a similar absent-mindedness in connection with another matter (Strasser, "Ueber die Methoden der Plastischen Reconstructionen," 'Zeitschr. f. Wiss. Mikros.,' Bd. iv, 1887, Hefte 2 and 3).

certain exceptions, connected with[1] the cranial ganglia of Vertebrates above Ichthyopsida, are rudimentary organs which only present themselves during embryonic life (Froriep (No. 17), Beard (No. 6), Béraneck (No. 10), and Kastschenko (No. 40).

The explanation so frequently given of such phenomena as this, viz. that such organs reappear in the ontogeny as pleasing reminiscences of the ancestral forms, if it has any claim to pass as an explanation at all, is only a partial one. There are many reasons for the reappearance of such rudimentary organs, one of which is the part they play in contributing to the formation of other organs. In fact, to come to the point, we are here dealing with cases of Kleinenberg's law of the development of organs by substitution (No. 41). I will not enter at length here into the application of Kleinenberg's law to the nervous system of Vertebrates. For a full comparison of the phenomena presented in the development of the Vertebrate nervous system with analogous and homologous phenomena in that of Annelids (No. 41), our knowledge of the former is as yet not sufficient. Some comparisons can even now be made, but the time for their consideration had better be deferred.

The neuro-epithelia of the rudiments of the branchial sense organs appear in the ontogeny of the higher Vertebrates, because they contribute certain form elements to the cranial ganglia, and very probably also to some, at least, of the sensory cranial nerves.

In the Chick (figs. 90—93, 96) such sense-organ rudiments are found in connection with the mesocephalic (figs. 90, 93, *m.g.*), trigeminus (figs. 90, 92, 94, v), facial (90, vii), glossopharyngeus (figs. 90, 91, ix), and vagus ganglia. In Mammals (sheep embryos) Froriep (No. 17) has described them in connection with the facial, glossopharyngeus, and vagus ganglia. In Mammals they have not as yet been described for the mesocephalic and

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[1] The exception here has reference to the nose and ear, for both of which organs evidence is accumulating for the views of their homology with the sense organs of the lateral line which I originally expressed (Nos. 4, 5, 6). I believe the organs of taste also arise from such neuroepithelium and wander through one, or in some cases perhaps two, gill-clefts on each side into the mouth cavity. My evidence for this conclusion will be produced in another Study.

trigeminus ganglia, but there can be little doubt that they also exist for these at some stage or other.

After the fusion of the mass of each cranial ganglion with the skin, form-elements are, as we have seen, given off into it. The ganglion leaves the skin, and, as in Sharks, almost certainly leaves sensory nerve branches behind it. The sense-organ rudiments afterwards disappear. I have not followed the steps of this process in the Chick, but I cannot doubt the general accuracy of Kastschenko's account (No. 40, pp. 281—284), for it agrees fairly well with Professor Froriep's earlier researches (No. 17) on the fate of the rudiments in Mammals.

This finishes the general account of the first formation of cranial ganglia in the Chick.

III. The Development of the Anterior Roots of Spinal Nerves in Elasmobranchs.

In Balfour's account of the spinal nerves in Elasmobranchii (Nos. 1 and 2), he described the anterior roots as direct cellular outgrowths from the lateral ventral region of the spinal cord, and in the second volume of the 'Comparative Embryology,' p. 372, he says: "The anterior roots of the spinal nerves appear somewhat later than the posterior roots, but while the latter are still quite small each of them arises as a small but distinct concise outgrowth from the ventral corner of the spinal cord, before the latter has acquired its covering of white matter. From the very first the rudiments of the anterior roots have a somewhat fibrous appearance and an indefinite form of peripheral termination, while the protoplasm of which they are composed becomes attenuated towards its end. They differ from the posterior roots in never shifting their point of attachment to the spinal cord, in not being united to each other by a commissure, and in never developing a ganglion." The anterior roots grow rapidly, and soon form elongated cords of spindle-shaped cells with wide attachments to the spinal cord." And in a note at the foot of p. 372: "The cellular structure of embryonic nerves is a point on which I should have anticipated that a difference of opinion was impossible, had it not been for the fact that His and Kölliker, following Remak and the older embryologists, absolutely deny the fact. I feel quite sure that no one studying the development of the nerves in Elasmobranchii with well-preserved specimens could for a moment be doubtful on this point. And I can only explain His's denial on the supposition that his specimens were utterly unsuited to the investigation of the nerves. I do not propose in this work entering into the histogenesis of nerves, but may say that for the earlier stages of their growth, at any rate, my observations have led me in many respects to the same results as Götte ('Entwickl. d. Unke,' pp. 482—483), except that I hold that adequate proof is supplied by my investigations to demonstrate that the nerves are for their whole length originally formed as outgrowths of the central nervous system. As the nerve-fibres become differentiated from the primitive spindle-shaped cells, the nuclei become relatively more sparse, and this fact has probably misled Kölliker. Löwe, while admitting the existence of nuclei in the nerves, states that they belong to mesoblastic cells which have wandered into the nerves. This is a purely gratuitous assumption, not supported by observation of the development."

I could have been content to leave this matter of the anterior roots unnoticed but for two circumstances. In the first place the figures which Balfour has given of their development in the 'Comparative Embryology' (vol. ii, p. 371, fig. 267), "Elasmobranch Fishes" (Pl. X, fig. 7), and in the paper on the spinal nerves (No. 1, Pl. XVI, figs. *Da. b.* and *c.* Pl. XVII, figs. *H* II, *I* II, and *E. b.*) are very diagrammatic, and His would be justified from his standpoint in objecting to their representing the true facts. On the other hand, I can raise the same objection to the diagrammatic figure of the development of anterior roots in Pristiurus, which His represents on p. 393 (No. 34, fig. 1) of his recent work. Nay, I cannot help insisting that if Balfour's figures were not what one might expect, His's figure is incorrect to a far greater degree, and the "Ehren-

Wache" of parablast cells which Professor His, in conformity with his peculiar doctrines, gives the nerve, has, so far as I can find out in Pristiurus and other Elasmobranchii, no real existence in the world of fact. I should have been quite satisfied but for these considerations to merely echo Dr. van Wijhe's recent remark on this point (No. 63, p. 76, Anmerkung). He says, "In Betreff der zelligen nicht faserigen Struktur der ventralen Wurzeln bei ihrem ersten Auftreten muss ich Balfour vollständig Recht geben."

There are three investigators who have regarded the motor-nerve formation as entirely due to fibres alone, without the inclusion of any nuclei. The view is one which can only be accepted if rigidly proved, and this in my opinion has not yet been done. His holds that the anterior root-fibres are prolongations of cells which lie in the anterior cornu of the spinal cord. Thus, according to him, a motor nerve-fibre passing from the spinal cord to a muscle in the foot would be a direct prolongation of a ganglion-cell within the cord, and no cell nuclei would at any time intervene in its course (Nos. 32 and 33, p. 375).

He asserts (No. 29, p. 475), "Mit Beginn des vierten Bebrütungstages, sind vordere Wurzeln erkennbar als Bündel feiner, vom Rückenmark aus in die Leibeswand tretenden Fäden. Vom ersten Moment an, da sie überhaupt sichtbar sind, haben sie die angegebenen Eigenschaften und ihrem Auftreten gehen keine zelligen Urgebilde voraus."

And again, in the more recent work (No. 33, p. 375), "Die peripherisch auswachsenden Fasern, sowohl die motorischen, als die sensibeln, sammeln sich als kurzen Stämmen. Jeder dieselben besteht aus einer Anzahl feiner kernloser Fäden, die in der Nähe des Ursprungs eine deutlich fibrilläre Streifung zeigen. Innerhalb eines Stammes zeigen die Fasern theilweise verschränkten Verlauf. Parablasticshe (!) Zellen zeigen sich beim menschlichen Embryo Anfangs nur sparsam zwischen den Nervenfasern zerstreut . . . . . . Je jünger ein Nervenstamm, um so kürzer ist er, das Auswachsen geschieht allmählich und es vergehen einige Wochen bis z. B.

die letzten Enden der Finger und der Zehen ihre Nerven erhalten haben."

To return to my own observations. I have as yet only investigated Sharks and Lizards on this point. The results, so far as they concern the latter group, will be given later along with observations on the anterior roots of the cranial nerves. Figs. 58, 60, 62, 53, 54, 56 and 61, on Pl. XIX, are intended to illustrate the development of anterior roots of spinal nerves in Elasmobranchii. One of the very earliest stages in the development of an anterior root (*a*) is shown in fig. 58 (Pristiurus), and it possibly corresponds to the stage figured by Professor His in the paper quoted above (No. 34, fig. 1). There is no possibility of recognising "parablastic" cells in this section, and one sees that while the root is partially fibrous there is at least one nucleus passing out of the spinal cord, either entirely or partly after cell division. A slighter later stage is represented in figs. 60 and 61. The fibres of the nerve have reached the muscle-plate,[1] but there are also two nuclei visible in the nerve-cord lying partly also in the cord. There are here also plenty of mesoblast—pardon, "parablast" cells in the neighbourhood. But they are not destined for the nerve, but are about to enclose the notochord to form the body of the vertebra.

Later stages in the development are figured in figs. 54, 56. Here, too, the fibrous nature of the nerve is very obvious, but one also observes a vast number of nuclei within the nerve, which one cannot regard, from their form and characters, as otherwise than offsprings of the nuclei which have passed at earlier stages, and even still continue to do so (figs. 60, 54, 61), from the anterior cornu to the nerve. When His regards the nuclei here present as mesoblastic or "parablastic" cells, his view is just as much a gratuitous assumption as the whole parablastic doctrine, as the Zwischenstrang ganglionic formation in the trunk, and as the identification of a certain ganglion

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[1] The end plates of muscles (and of the electric organ) are derived from ganglionic cells, which wander in this way in these early stages from the anterior horn to the muscle-plate. Several figures show this, and I shall treat of the matter at length elsewhere.

to be mentioned elsewhere as the ciliary ganglion. A figure such as Professor His gives in his recent work of two fibres passing out from two nuclei in the anterior cornu of the head, outside which they receive an "Ehren-Wache" of four "parablastic" cells, two on each side, is one which, in spite of much search, I have never seen. On the other hand, the figures I give in Pl. XIX could be multiplied by the dozen, and figs. 53 and 58 are representations of an appearance which I have often met, and which Dr. van Wijhe assures me he also has very frequently seen. From these facts, and from facts regarding the development of anterior roots of cranial nerves, and nerves of the sense organs of the lateral line or branchial sense organs, I do not for a moment hesitate to declare that the facts of development are contradictory to (1) Professor His's view of the absence of nuclei in the anterior roots, and (2) his assumption that when such nuclei are present they are of "parablastic" origin. It is worthy of notice that in his original assertions Professor His absolutely (vide supra) denied the presence of nuclei in the anterior roots, and only now that their presence in those structures in Elasmobranchii is obvious to every observer, including Professor His, does it occur to him to make use of that wonderful doctrine of parablast to explain their presence. Professor His's attempt to get out of a false position here is only a little more dignified than his endeavour to explain away the meaning he attached to the Zwischenstrang.

IV. The Ganglionic Development in Different Groups of Vertebrates.

Without anticipating the results of my researches on other groups, which so far include Teleostei, Lizards, Frog, Newt, and Rabbit, I may be at least allowed to say now that the above mode of development of cranial and spinal ganglia holds, with very slight and unimportant modifications, for all these forms also. I might have left these forms undescribed but that for the certainty that some observer or other would by-and-by quote their development according to his ideas, as opposed to the facts I have here described for Elasmobranchii and Birds. The conviction was very early in the research forced upon me that the development of spinal and cranial ganglia in all Vertebrates must take place after one type, and any differences found in different groups must be referable to variations or changes rung on that type. And as an example, the investigation of the development of cranial ganglia in the Anurous Amphibians was one I could not leave unnoticed on account of Spencer's notes on the matter (No. 59). All the more, as in my paper on the branchial sense organs (No. 6) I felt obliged, after the examination of some of Spencer's preparations, and of a few I made myself, to support his conclusions. We were then both in error on one point—of that I am now quite sure—and that is in reference to the deeper layer of epiblast above the level of the lateral sense-organ thickening, and which connects the latter in early stages with the neural plate. We both believed it gave origin to the trunk of the nerve. This is not so. That layer is indifferent except at two points corresponding exactly to the two points at which the ganglionic form elements arise in Elasmobranchs. In fact, as a preliminary note I take the opportunity of saying that the cranial ganglia of the Frog develop in exactly the same way as those of Elasmobranchii. Among other forms examined the Lizard is one of the most favorable for such investigations. It also agrees essentially in the mode of development of cranial and spinal ganglia with Elasmobranchii.

The Newt has been mainly studied by Bedot (No. 9), and Misses Johnson and Sheldon (No. 38).

In both of these works I shall have occasion to underline a number of mistakes and false interpretations; here I will only remark that I am somewhat surprised that none of these investigators have seen the epiblastic origin of the spinal ganglia in this animal. I know no animal in which such origin is easier to identify. The criticisms with which the two latter authors have seen fit to honour my work may also be here left unnoticed. The only one whose justification I will acknowledge is their doubt of the accuracy of Spencer's and my investigations on the origin of the root of a cranial nerve in the Frog. I have admitted the error above, and need not here mention the matter further. To one assumption of these two authors (No. 38, p. 11) I must, however, be allowed here to reply. They remark: "More recently the theory of the derivation of the whole or greater part of the cranial nerves from the epiblast has been supported by Mr. Spencer and Mr. Beard. This view is a revival of that held by Götte."

(1) The origin of a part of each of the cranial ganglia, and of what I called the suprabranchial nerves, was no longer a theory after the publication of my paper on the branchial sense organs (No. 6). It was then demonstrated for certain parts of the cranial ganglia[1] and for certain nerves that they have an epiblastic origin, and the matter could for these hardly be called a "theory." I can now demonstrate that the whole of the components of the various cranial ganglia are epiblastic in origin, and not wholly or in part outgrowths of the central nervous system.

(2) Götte never held this view, whatever may now be the case. I can only suppose that the two ladies never read the passages in his work which bear upon the question. The following quotation from Götte's 'Unke' (No. 22, p. 719) gives a clear statement of Götte's conclusions at that time:—Bei der Untersuchung der Kopfnerven handelt es sich zunächst um ihre Zugehörigkeit zu den ganzen hintereinander liegenden segmentalen Abtheilungen des Kopfes ferner um ihre Unterscheidung nach dem Ursprunge aus dem inneren oder aüsseren Segmente des mittleren Keimblattes oder aus anderen Embryonalanlagen jeder Abtheilung. Zu den letzteren gehören der Sehnerv und die Seitennerven als Erzeugnisse des oberen Keimblattes, die übrigen Kopfnerven enstehen aus dem mittleren Keimblatte."

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[1] I was inclined then to regard the whole of the ganglion as arising from the epiblastic sense thickening, and the cells derived from the "neural crest" as forming the root of the nerve. The point is a very difficult one to decide, and I refer the reader to a discussion of it in another part of these researches.

V. The Neural Ridge.

The reader may have remarked in the preceding pages that the terms neural ridge and neural crest have been banished from my account of the development of the ganglia, both cranial and spinal. The reasons for this may now be explained, and hand in hand with this explanation one may compare the origin of the ganglionic Anlagen as described here with the accounts of previous observers.

Considering for a moment the neural ridge without prejudice as to its origin, most authors, following Marshall (No. 46, p. 15), regard the neural ridge as a continuous structure passing forwards from the mid-brain right away backwards through the head and along the whole spinal cord as a continuous structure; and from its continuity in all parts, of which in a certain sense there can be no doubt, Balfour and Marshall were inclined to attach great morphological importance to it. The continuity of the neural ridge is originally most marked in the head, in which the ganglia show tendencies to concentration and fusion, and where also the ganglionic Anlagen are very large.

In the spinal cord, on the other hand, where the ganglionic Anlagen are not so massive, the continuity of the neural ridge is by no means so evident as in the brain. Indeed, from the neural-ridge stage onwards, and even from the very first formation of the spinal ganglia Anlagen, the segmental nature of the latter is one about which a careful investigator can make no mistake. For this reason, and the additional one that all the cell elements of the neural ridge in both head and trunk undoubtedly, as His insists (No. 34, p. 393), pass over into the ganglia, I can see no particular advantage in the use of the term. And when one comes to consider, as we shall presently do, the origin of the neural crest, my objections to the term as at present used are intensified. Marshall, from the apparent fusion of the neural ridges of the two sides, gave to the single structure thus formed the name of neural crest. Here, again, as the structure is certainly a bilateral one and not unpaired, and as in many cases its bilateral structure is very evident (figs. 21, 24, 46, 51), I confess I see no convenience in the use of a name to which doubtful morphological characteristics are attached.

We are now met by the question, Assuming that the ganglia arise as outgrowths of the neural ridge, what is the ultimate origin of the structure, and are the ganglia first visible in the neural-ridge stage?

The foregoing researches give the answer to this question, and in anything like a complete and correct form they are the first researches which can lay claim to decide the question. Six years ago Sagemehl (No. 56), in a prize research, published observations which he believed, and apparently the judges of the competition also, to be a solution of the problem, so far as the spinal ganglia are concerned. How little claim his researches have to pass as a last word on the origin of the ganglia will be evident to the reader of this paper, and if he will take the additional trouble to compare the numerous figures I have given here of Elasmobranchii and the Chick with the nineteen figures of Sagemehl's work, he will, I think, admit the correctness of my conclusion, that Sagemehl never saw any of the earliest stages of the formation of spinal ganglia. Except for Marshall's and Onodi's researches on the cranial ganglia of the Chick, this remark applies to all the observations of various investigators of the development of cranial and spinal ganglia. His (No. 29) has also seen, but only partially interpreted in a correct sense, some of the earliest stages in the cranial nerves of the Chick. As His's Zwischenrinne theory was one of the earliest on the development of cranial nerves, we can at once consider his claims to having furnished the solution to the above question in the wider sense of the origin of the ganglia Anlagen. Remak's (No. 54) older observations, originally supported by Balfour and Foster, may be here passed over, for no one now believes that the ganglia arise as differentiations of the "protovertebræ." And the same also holds for Hensen's conclusions (No. 24), which are more of a theoretical nature than results of actual investigation; still, as I shall elsewhere show, there is an element of truth in Hensen's suggestions, though not quite the same Hensen thought.

It is perhaps unkind to remind Professor His that his "Zwischenstrang" was originally believed by him to be concerned in the formation of the urogenital system. The Zwischenstrang was afterwards converted in the basis of a theory of the origin of the spinal ganglia. In spite of the persistent way in which Professor His, without full and complete investigation of the matter, holds to this Zwischenstrang theory of the proved origin of spinal ganglia, a persistence which leads him in his recent work (No. 34, pp. 391 and 416) to identify it with what Balfour, Marshall, Sagemehl, and others have regarded as the first stages in the formation of the ganglia, and to rebaptize the structure, which undoubtedly exists (figs. 97, 98, 99, *z.*), under the name of "Ganglionstrang,"[1] I do not see how Professor His can escape the fatal consequences of the researches I now record.

I think I have demonstrated, even to Professor His's satisfaction, that the Zwischenstrang is just that part of the epiblast which takes no part in the ganglionic formation, and that it owes its formation to the cutting out of ganglionic Anlagen between it and the neural plate. As the crowning proof that the Zwischenstrang is not identical with the neural ridge or the

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[1] Professor His (No. 34, p. 417) states that both olfactory and auditory organs of Vertebrates take their origin from parts of the "Zwischenrinne" or "Ganglienrinne" which remain open. This is absolutely incorrect. The views of the homology of both these organs with the lateral or branchial sense organs, which I formerly advocated (Nos. 6, 5, 4), can be still maintained. From figures in my former work (No. 6) and figs. 25, 27, 46 of this paper, it is obvious to any unprejudiced observer that the auditory organ develops ganglionic elements from two sources, just as occurs in a typical gill-bearing segment. The same holds for the olfactory organ. I postpone for the time the further elucidation of my views of the homology of these two sense organs, but only for a time, for I intend shortly to discuss the problems they present more fully; here I will only say that no one has as yet urged unanswerable arguments against my views. Personally, I may remark, I care nothing about the quondam existence of gill-clefts for ear and nose; the important points to me are those which make the nose and ear parts of the system of lateral or branchial sense organs.

ganglionic Anlagen, I may refer to figs. 97, 98, 99 and others, more especially figs. 97 and 98, in which the "Zwischenstrang" and the ganglionic Anlagen can be seen in the same figure, and where they are entirely distinct and separate.

When we turn to Professor His's researches on the cranial ganglia of the Chick (Nos. 28 and 29), we find that he was a little more fortunate in seeing some of the true facts. But here again his theory influenced his interpretation of the facts. The foldings of an elastic plate by which, as is well known, Professor His explained all embryonic phenomena[1] (No. 31), must also find their application in the formation of the cranial ganglia. It is not merely in the assumption of such a folding in of the epiblast of the head to form the ganglionic Anlagen in his "Zwischenrinne" that His is in the wrong; he has actually figured such a Zwischenrinne (No. 29, Pl. XVII, figs. 3, *b*, *c*, *d*, *e*, *f*).

I have made a very large number of sections through the head region of Chick embryos (well preserved) in this stage, and as the result I do not for a moment hesitate to say that the Zwischenrinne of His has no existence. On the contrary, in the head just as in the trunk, as the result of the separation of the ganglionic Anlagen from the epiblast, a "Zwischenstrang" may be formed (figs. 63, 97, 88); but this structure also plays no part in the formation of the ganglia. If Professor His had not assumed or believed in the existence of this "Zwischenrinne," and if he had left the "elastic plate" out of question and acknowledged the proliferation of a certain portion of the inner epiblastic layers to form the ganglia, he, who certainly was the first to see some of the true appearances on the Chick, would also have been the first to ascribe their true epiblastic origin to the cranial ganglia. But under the dominance of his theory he believed he saw structures[2] which

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[1] This "Mechanische Auffassung" has unfortunately more influence on Professor His's results than his conception of the great value of comparative embryology, to which he lays claim in p. 405 of his recent critical study.

[2] One must bear in mind that the sections of those days were nothing like as good as those a fair worker can now make.

have no existence; and he says in a passage which on another page I have quoted in full, "Ich verwerfe überdies, wie ich schon an anderem Orte ausgesprochen habe, das von manchen Embryologen so freigebig benutzte Princip der lokalen Wucherungen" (No. 34, p. 465). The reference to another place in this passage is to the "Briefe über unsere Körperform" p. 67, *u. f.*—a work in which the foldings, &c., of an elastic plate are used to explain fully the development of all the organs of a Vertebrate embryo. By this declaration Professor His gives the coup de grâce to any possibility of the acceptance of his account of the cranial ganglia in the Chick as a solution of their origin. The two diagrammatic figures which are represented on p. 465 of Professor His's paper on the peripheral nervous system have been referred to recently (No. 34, p. 394, Anmerkung) by him as representing really the true facts, and as agreeing essentially with the results of other investigators; but that I may not be accused of an unfairness, which is far from my thoughts, I quote the passage: "Wie jedes Schema, so ist auch dieses in Betriff absoluter Correctheit[1] anfechtbar, aber, dass die untere Lamelle des dort ausgebogenen Streifens mit der von Kölliker, Sagemehl, u. A. abgebildeten Ganglienanlage zusammenfällt, bedarf kaum eine Erlaüterung." As these figures show an epiblastic invagination to form the ganglionic Anlagen, in conformity with the elastic plate theory, —an appearance which has no existence in fact,—it is difficult to see how the lower layer of this structure can be identical with the ganglionic Anlagen of Kölliker, Sagemehl, and others. This is as near being the case as any fancy figure drawn in the same position would be. The principle of the epiblastic origin of the ganglia, apart from the central nervous system, is one on which His has long been in the right; the mode in which he believes this origin takes place is one in which he has been further from the true facts than anyone else. I have quoted before the following passage from Professor His's recent paper (p. 380), and as we now see that the facts are not so much

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[1] This "Schema" of His's is not relatively correct, it is absolutely incorrect!

matters of agreement as Professor His supposes, one may quote it again with the request to Professor His to furnish us with the evidence in which he bases his opinions on the origin of the ganglia from the Zwischenstrang and Zwischenrinne, and of the olfactory and auditory organs from parts of the latter structure which remain open (No. 34, p. 417). These are questions of facts whose accuracy I challenge. Nor are they the only points of fact on which I (and many others) disagree with Professor His. Of that more elsewhere.

The passage reads: "Bei genauerem Zusehen findet man eben, dass die Differenzen nicht in dem liegen, was der eine und der andere Beobachtungskreis an thatsächlichen Befunden ergiebt, sondern in demjenigen, was die Vertreter der einen und der anderen Schule zwischen die Zeilen zu lesen sich bemühen. Nun sind aber die jüngeren vergleichend morphologischen Schulen in der Lectüre zwischen den Zeilen über die Maasen weit gegangen, und ich halte es für eine Pflicht, meinen Bedenken hiergegen offenen Ausdruck zu geben."

However it may be with the hypotheses, &c., one thing is certain, that some of Professor His's most fundamental facts are no facts at all, and we may not unnaturally ask whether the reproach intended for us younger morphologists does not partially recoil on Professor His himself?

All other observers, excepting Spencer for the cranial ganglia of Amphibia, are agreed in referring the source of the posterior roots and ganglia to the neural ridge of Marshall, and nearly all agree with Balfour's maxim of the origin of the latter structure as an outgrowth from the central nervous system.

On p. 369 of the 'Comparative Embryology' of Balfour, vol. ii—a book which represents his latest views on the question—we read: "All the nerves are outgrowths of the central nervous system;" and on p. 374, "The neural crest clearly belongs to the brain, from the fact of its remaining connected with the latter when the medullary tube separates from the external epiblast."

Marshall's position is not quite so simple. The cranial nerves (and ganglia) of the Chick Marshall (No. 46) refers to the re-entering angle between the neural plate and external epiblast, but nothing definite is stated as to the relations of this portion of the epiblast to the external epiblast on the one hand or to the brain on the other. In other words, if we are entitled to conclude that Professor Marshall held the independent epiblastic origin of cranial nerves and ganglia, we miss in the account the necessary denial of Balfour's view as stated above. If Marshall recognised the epiblastic origin of the neural ridge he did not tell us whether or not he holds with Balfour that it "clearly belongs to the brain." This is important, for taken in connection with his acceptance of Balfour's view of the origin of spinal ganglia, it does not preclude the possibility of the assumption that the neural ridge in the Chick arose from a portion of the brain which has not got shut in. Professor Marshall has indeed seen and described part of the true origin of the cells which form the neural ridge in the Chick. The whole of the source he has not identified, and he did to draw the conclusions of the independent origin of the ganglia to which he was entitled.

The part he had not seen is that portion of the cranial ganglion Anlage which is formed from the external epiblast outside the angle between epiblast and brain. This was first seen by Onodi (No. 51).

Judging from the following passage, it would appear as though Professor Marshall held the origin of the ganglia to be the same in both brain and cord, and the difference to be only as to the time of closure of the neural canal. He says (No. 46, p. 16): "Its (the neural ridge) first appearance precedes the closure of the neural canal, but after about the fortieth hour the closure of the canal proceeds backwards more rapidly than the growth of the neural ridge, so that in the greater part of the length of the spinal cord the ridge is developed as an outgrowth from the summit of the cord itself, and never has any connection with the external epiblast."

In order to get a little nearer Marshall's position I turned to his latest statements on the development of nerves, and find (No. 50, p. 9) that he quotes with approval Balfour's views. He says, "Balfour showed that, contrary to the generally accepted theory, the nerves are outgrowths from the central nervous system, and therefore of epiblastic origin, instead of being, as formerly supposed, structures arising independently in the mesoblast and only acquiring a secondary connection with the brain and cord." Hensen (No. 25), Kölliker (No. 43, p. 621), Sagemehl (No. 56, p. 33), van Wijhe (Nos. 60, p. 18), Bedot (No. 9, p. 186), Shipley (No. 58), Béraneck (Nos. 10, 11), and Misses Johnson and Sheldon (No. 38), have practically accepted Balfour's and Marshall's views; and van Wijhe (No. 61, p. 4) has used the conclusion as an argument against my views of the epiblastic origin of the sensory nerves of the branchial sense organs (Beard, No. 6, p. 69). He remarks, "Wenn Beard jetzt, seiner früheren Behauptung entgegen, den Olfactorius und die Seitennerven nebst ihren Ganglien allein aus der Epidermis enstehen lässt, so kann er dies wohl nei beweisen weil der Stamm der Nerven sich ursprünglich aus dem Medullarrohre entwickelt."

It is not difficult from the researches I have here recorded—and others as yet unpublished—to conclude that all these authors have been mistaken in describing the ganglia as outgrowths of the central nervous system. The figures I have given demonstrate the justice of this criticism, and as a final argument, which more especially negatives Balfour's remark (quoted earlier), that the neural crest clearly belongs to the brain, I will point out that the limits of the two structures, brain and ganglionic Anlagen, are very early sharply separated off by a well-defined line (figs. 45, 51, 32—36 and others), and only in those stages in which the neural plate is quite open, in fact only during the primitive-streak period can one really, with any pretence to accuracy, speak of a common Anlage for both structures, of an encephalo-ganglionic Anlage. But this is a stage at which the embryo is barely differentiated into the three embryonic layers.

Onodi (No. 51) has shown the true source of origin of the main portion of each cranial ganglion in the Chick,—of that portion which is not derived from the remains of the branchial sense organs. The rest of his researches, on the cranial and spinal ganglia of Elasmobranchii, Teleostei, Lizards, and Mammals, and on the spinal ganglia of the Chick, lead him to the same results as Balfour, Marshall, and others. His researches hence agree partially with my own for parts of the cranial ganglia of the Chick, but for all other types he has failed to see the true epiblastic origin of both cranial and spinal ganglia.

Hoffmann (No. 36, pp. 45—49) while supporting Balfour's views of the outgrowth of spinal ganglia from the cord, considers it probable that the posterior root ganglia of the cranial nerves of Teleostei arise from the epiblast beyond the limits of the neural plate, and before the closure of the latter. He did not prove that such was the case.

In later researches (No. 37, p. 204) he again refers to the neural ridge, but says nothing of its origin.

VI. THE GROWTH OF OUR KNOWLEDGE OF THE INDEPENDENT EPIBLASTIC ORIGIN OF THE PERIPHERAL NERVOUS SYSTEM.

The first conclusions on this question were arrived at by Götte (No. 22, p. 72) and Semper (No. 57, p. 256), both of whom stated that the lateral nerve has an epiblastic origin and arises pari passu with the growth of the lateral line as a differentiation of the epiblast. Götte (p. 719) extended this mode of development to the nerves of the lateral sense organs of the head. These statements, on which doubt was cast by Balfour, were practically confirmed by van Wijhe (No. 60, p. 35) and Hoffmann (No. 36, p. 89,) for Teleostei. I (No. 4) believed Balfour's doubts to be well founded, but in two subsequent publications I was able to prove, for Elasmobranchii the accuracy of Semper's account. Just before my paper on the origin of the cranial ganglia (No. 5) appeared Professor

Froriep published his researches on the rudiments of sense organs in connection with several cranial ganglia in Mammalia (No. 17). Without committing himself very definitely to the matter Professor Froriep did not think it impossible that the ganglia derived form-elements from the epiblastic fusion (No. 17, p. 40), and the cranial ganglia concerned were regarded by him as the remains of the ganglia of sense organs which in the course of phylogenetic development had got lost.

He says (p. 45): "An der drei Nerven übereinstimmend gehen aus der Kiemenspaltenorganen keine definitiven Bildungen hervor, was von ihnen übrigbleibt, ist lediglich die gangliöse Anschwellung des Nerven, welche ursprünglich die nervöse Unterlage des Sinnesepitheliums gewesen ist. Diese Ganglien, Ggl. geniculc, Ggl. petrorsum, und Ggl. nodosum, sind demnach als rudimentäre Organe zu betrachten, sie stellen die Ueberreste phylogenetisch verlorengegangener Sinneswerkzeuge dar."

Professor Froriep was undoubtedly the first in point of time to describe this fusion of cranial ganglia with the epiblast, and to draw the conclusion that the modified epiblast at the point of fusion was the remains of a special branchial sense organ. He hesitated (p. 35, et seq.) to homologise them with the sense organs of the lateral line in Fishes, considering it possible that they corresponded with rudiments of other sense organs connected with the ventral branches in Fishes as in Mammalia, and which, as in Mammalia, probably disappeared in later development.

The identification of the ganglion fusion with the "Anlagen" of the sense organs of the lateral line for head and trunk in Elasmobranchii, was first made by me (No. 5) independently of Professor Froriep, and at that time also—a point which I afterwards developed more fully—I was quite aware of the relations of the sense organs to the gill-clefts, for I homologised the nose with such a ganglionic epiblastic fusion, and called it "the modified sense organ of a gill-cleft rather than a gill-cleft itself;" and in my note-book there still stands the notice from which I wrote that conclusion, which shows, I think, very clearly that, contrary to Professor Froriep's recent criticism (No. 19, p. 821), I was then fully aware of a point to which he attaches a very great deal of importance, viz. their typical position over a gill-cleft. The note is, "The nose is not a gill-slit but the sense organ which sits above a cleft."

In my paper on the branchial sense organs (No. 6) I showed that out of this epiblastic fusion, which (No. 5) I had described independently of Froriep, the sense organs of the lateral line or branchial sense organs take their origin. The sensory epithelium grows in various directions by division of its cells, and it pushes away the indifferent epiblast. From the sensory epithelium arise both sense organs and the nerves which supply them and connect them with the ganglia. The ganglia were considered as mainly arising from the thickenings, the cells derived from the neural ridge only forming the root of the nerve. Whether the latter conclusion is true or not I cannot say, certainly some of those cells do take part in the formation of the nerve, and their nuclei may be found along the course of the nerve. The suprabranchial nerves were distinguished from the præbranchial and postbranchial, and a morphological importance was attached to the former. At the present time I regard the nature and mode of origin of suprabranchial, præbranchial, and postbranchial nerves, so far as the latter innervate the sense organs (for, as is well known, they also contain motor fibres to the muscles of the gill-cleft) as entirely the same, and would now say all the nerves to the sense organs of the lateral line or branchial sense organs are derived from the neuro-epithelial "Anlagen" of the latter.

Nothing was said in my former paper of the origin of the neural-ridge of the spinal nerves, which lay beyond the scope of my researches at that time. Nose and ear were considered as modified branchial sense organs and their ganglia (for, in spite of Gegenbaur, the nose[1] has a ganglion) as differentiations of the sensory epithelium. Rudiments of such branchial sense organs and their ganglionic fusion were described in three-days'-Chick embryos. Spencer (No. 59) on Amphibia (Frog),

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[1] See No. IV of these Studies.

derived the cranial ganglia from the epiblastic thickenings which form the lateral sense organs, and the main roots of the nerves from the inner epiblast connecting this thickening with the neural plate. This latter conclusion, which I formerly supported, is wrong.

Onodi (No. 51) extended Marshall's (No. 46) description of the origin of the cranial ganglia in the Chick from the angle between the epiblast and the neural plate, in that he stated that the epiblast outside this also shares in the formation. Neither Onodi nor Marshall distinctly say whether they regard this portion of epiblast as part of the central nervous system or not. And, as we have seen for the cranial and spinal ganglia of other forms, they supported Balfour's views.

In a note which I quoted in the introduction, van Wijhe (No. 61) mentions that the olfactory nerve arises from an epiblastic differentiation at the lips of the anterior neuropore. The present research, taken in connection with my former paper on the branchial sense organs, shows that the sensory nerve-elements of the whole of the peripheral nervous system arise as epiblastic differentiations independently of the central nervous system.

VII. The Relations of Cranial to Spinal Ganglia and of the "Seitenorgane" of Annelids to the Sense Organs of Vertebrates.

It is far from my intention to enter here into the discussion of morphological questions. My contribution to recent controversy may fitly find a place in a special paper in which I intend to analyse the recent critical studies of Professors Gegenbaur and His on Vertebrate morphology, and especially on the nervous system.

But still, the conclusions to which Froriep and I arrived at regarding the fundamental differences which obtain between the head and trunk regions of Vertebrates may be here slightly reviewed, and, so far as I am concerned, revised in the light of the facts recorded in the preceding pages. Gegenbaur

(No. 20), and in a certain sense Dohrn and others, regard the head as a specially modified portion of the trunk, and, as is well known, Gegenbaur (No. 20) considered that certain of the cranial nerves could be reduced to spinal nerves. His present position with regard to recent researches is defined more or less clearly in his recent paper (No. 21). I cannot now enter into a criticism of that—the limits of my space forbid it,—and, as far as possible, I have endeavoured to shut speculative matter out of this research.

Dohrn (No. 13, p. 471) has formulated his conclusions as to the relations of the spinal and cranial nerves and ganglia in the following passages:—

"Die Hirnnerven haben diejenigen Leitungsbahnen verloren, welche die Urwirbel und deren Derivate innervirten; sie haben aber in Folge der ausserordentlichen Vergrösserung und Complicationen der visceralen, i. e. ventralen Theile des Kopfes um so mehr gewonnen und sind durch die vielfachen Verschiebungen der bezüglichen Theile in ihrem Verlaufe sehr verwickelt geworden.

Die Spinalnerven ihrerseits haben am Rumpfe in ihren visceralen Verrichtungen Verschiedenes verändert (—auf welche Weise soll später dargestellt werden—,) haben aber durch die Entwickelung der Körper—und Extremitäten—Musculatur im Umfang im Allgemeinen nicht vermindert, und sind in gewissen Sinne weniger modificirt, als die Cranialnerven. Am Schwanz dagegen haben sie durch die Einbusse der gesammten Visceralpartien die stärksten Verluste erlitten und sind dort demgemäss am wenigsten complicirt."

While there are some points in the above statements with which I can express my agreement, my standpoint is more on Froriep's side than on that of Dohrn. For a general survey of Froriep's views I must refer the reader to that investigator's recent utterances (No. 19, p. 833, et seq.).

I agree with Professor Froriep that at present we cannot see much beyond the primitive separation of the Vertebrate body into two sharply-defined regions,—a respiratory region the head, and a locomotive (and digestive) region the trunk.

We have hardly begun to get any idea of the more primitive structures from which these two regions are derived.

I have previously with Froriep, much to the disapproval of Gegenbaur, His, Dohrn, and Eisig (No. 15), sharply contrasted the cranial and spinal nerves and ganglia, and declared my conviction (No. 6) that it is a very doubtful question whether the two sets of organs ever had the same primitive characters. The development of the branchial sense organs and ganglia, in connection with the cranial ganglia, was my main consideration for saying this. And the same considerations appeared to Froriep (independently) to add strength to this conclusion at which he had arrived some years ago (No. 16).

The question arises, How is the position altered by the researches I now record?

Eisig (No. 15, p. 542) had, perhaps rightly, urged against my views that it was not impossible that the spinal ganglia of Vertebrates represent the "Seitenorganen ganglia" of Capitellidæ. Without devoting here the time which a thorough examination of Dr. Eisig's comparisons entails, I cannot omit a partial discussion of this point. The exact weighing of the pros and contras of Dr. Eisig's views must be left over for another publication, in which we must examine more closely the lateral sense organs of Vertebrates.

I quote the following passage from Eisig's great work[1] (No. 15, p. 542), in spite of its length, because it touches upon the proposed homology between the spinal and cranial ganglia on the one hand, and the parapodial ganglia of Annelids on the other. This homology, as I previously mentioned, was suggested by Kleinenberg (No. 41, p. 220), and in a strict morphological sense I think, as the result of my researches, it can be accepted.

The passage runs thus (p. 542): "Es muss dagegen speciell der Punkt von mir erörtert werden auf den sich Beard zum Behufe der Perhorrescirrung der Homologie von Gehirn und Spinalnerven stützt: nämlich, die Thatsache, dass die Spinal-

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[1] I take this opportunity of expressing my gratitude to Dr. Eisig for the generous gift of a copy of his immense monograph.

nerven nicht ebenso wie die Hirnnerven mit Hautsinnesorganen (Seitenorganen), respective mit Ganglien solcher in Verbindung träten. Um so mehr muss dieser Punkt ins Auge gefasst werden, als ich davon überzeugt bin, dass die in ihm enthaltenen Probleme auf dem Boden der Vertebraten-morphologie allein nicht gelöst werden können, indem es sich um Verhältnisse handelt, welche phylogenetisch so weit zurückliegen, dass uns nur die den vermuthlichen Ascendenten der Vertebraten näher stehenden Wirbellosen noch Anhalts-punkte für den Ausgang und die Richtung der bezüglichen Entwickelungen zu bieten vermögen.

" Wenn die Spinalnerven gegenwärtig nicht mehr ähnlich wie die Hirnnerven mit Seitenorganen, respective mit Ganglien solcher im Bereiche der Haut in Verbindung treten, so frage ich zunächst Beard, woher er denn weiss, dass dies auch früher nie der Fall gewesen sei, ferner frage ich ihn, ob er irgend einen triftigen Einwand gegen die Vorstellung beigebracht hat oder beibringen kann, dass die Ganglien der hinteren Spinalnerven wurzeln möglicherweise den Seitenorganganglien der Hirnnerven entsprechen? Wie berechtigt diese Frage ist, geht daraus hervor, dass nicht etwa nur Thatsachen der Vertebraten —sondern auch solche der Anneliden-Morphologie zu Gunsten einer solchen Vorstellung oder Hypothese sich anführen lassen."

Then follows the citation of Kleinenberg's views respecting the homology of the parapodial ganglia of Annelids and the spinal ganglia of Vertebrates, which I have already quoted in the introduction of this paper.

Dr. Eisig continues (p. 542): " Wenn man erinnert, dass ich ganz unabhängig von der vorliegenden Frage dazu gekommen bin, die Seitenorganenganglien der Anneliden von den Parapodialganglien der Anneliden abzuleiten, so wird man einsehen, dass unserem weiteren Schlussverfahren schon der Weg vorgezeichnet ist. Es entsprechen nämlich aller Wahrscheinlichkeit nach im Vertebratenrumpfe die Spinalganglien den Seitenorganganglien (Parapodialganglien) der Anneliden.

" Und auch die Frage, warum denn erstere Ganglien bei den

Vertebraten nicht mehr so wie diejenigen der Hirnnerven zu der Haut, respective den Seitenorganen ontogenetische Beziehungen aufweisen, lässt sich beantworten. Derselbe durch die Concentrirung des Kopfes oder Gehirnes hervorgerufene Prozess, der an den übrigen Bestandtheilen des Seitenorgansystemes so tiefgreifende Veränderungen hervorrief, nämlich, die Anbahnung einer einheitlichen und directen (Gehirn-) Leitung an Stelle der segmentalen, hat auch die ursprünglichen Hautbeziehungen der Seitenorganganglien (Spinalganglien) allmählig zum Schwinden gebracht. Nachdem einmal die directe Leitung zwischen dem Gehirne und dem Seitenorgansysteme des Rumpfes hergestellt, und die Innervation durch Spinalnerven zurückgetreten war, so lag auch keine Veranlassung mehr für Verbindungen zwischen Spinalnerven und Haut vor, und so können wir einsehen, dass die nunmehr für ihre Sinnesorgane ebenfalls bedeutungslos gewordenen Seitenorganganglien des Vertebratenrumpfes immer unabhängiger von den Seitenorganen und schliesslich den Spinalnervenwurzeln, respective dem Rückenmarke, einverleibt werden. Alles das ist zwar—es sei wiederholt—vorlaüfig noch durchaus hypothetisch, aber es gewänne schon in dem Momente solideren Boden, wo in der Entwickelungsgeschichte der Spinalganglien irgend eines Vertebraten noch Anzeichen von Hautverbindungen nachgewiesen würden, und wer möchte behaupten, dass unsere Kenntnisse bereits hinreichen, um die Existenz-möglichkeit einer derartigen Recapitulation a priori verneinen zu können? Wie dem aber auch sei, diese auf Thatsachen beruhende Hypothese zeigt, dass es angesichts der so verwickelten Verhältnisse doch nicht an Anhaltspunkten für eine mögliche Lösung fehlt, und die Aussicht auf eine mit Schwierigkeiten verbundene Lösung ist doch erfreulicher, als die auf gar keine. Gar keiner Aussicht auf Lösung kommt aber die Auffassung Beard's gleich, welche, da sich zwischen Rumpf und Kopf zahlreiche Divergenzen ausgebildet haben, die Vergleichbarkeit beider überhaupt in Frage stellt."

The above extracts naturally fall into two divisions. In the first place there is the question of the actual facts of development which Dr. Eisig puts to me, and in the second place there is the answer which Dr. Eisig from his standpoint gives to these questions. With the latter I am here little concerned, for the answer is purely hypothetical, as Dr. Eisig admits, and no one can object to his right to establish as an admitted hypothesis the view that the lateral sense organs were once connected with spinal nerves. According to my ideas the evidence is entirely wanting, and the quotations from three or four authors[1] which Dr. Eisig makes to show that even now spinal nerves send branches to the sense organs situate in the trunk, do not seem to me to affect the question; for, as I shall elsewhere show, they are all either vague or of a very doubtful character, and as yet no one has figured these connections.

These remarks also answer his questions as to whence I know that such connection was never the case. We know nothing of such connection of spinal nerves with the sense organs of the lateral line, either now or in the past, and any opinion one may express in favour of such a view is only an assumption.

To the second question, whether the spinal ganglia are not homologous with the sense-organ ganglia of the head, I think the answer must be decidedly in the negative.

I regret to be compelled to this result, but I see no way out of the conclusion that the spinal ganglia of the trunk are homologous with those portions of the cranial ganglia which take their origin in the similar position to the spinal, viz. just outside the lips of the neural plate. I have never as yet seen a trace of the sensory epithelium and ganglia of the sense organs in the trunk region of a Vertebrate embryo. Here, of course, I except the sense organs derived from the vagus which wander into the trunk, as I have shown elsewhere (No. 6, p. 19), by displacing the indifferent epiblast.

I have, moreover, never seen a trace of a sensory epithelium

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[1] The authors quoted are Julin (No. 39), Ransome and Thompson (No. 53), and Ryder (No. 55). While this paper was passing through the press, the supposed connection between spinal nerves and lateral nerve has been totally refuted by Professor Dohrn ("Studien, &c.," No. xiii, 'Mittheil. a. d. Zool. Station zu Neapel,' Bd. viii, Hft. ii).

in connection with the neural ganglia, i. e. in connection with those ganglia in head and trunk which are formed just outside the limits of the neural plate; and, as Froriep and I have indirectly shown, the lateral sense organ Anlagen in higher Vertebrates show no disposition to leave their original home above the gill-clefts, and to wander into the epiblastic Anlagen of the neural ganglia, but force the latter, as it were, to come to them to receive their contingent of nerve-cells.

Like Dr. Eisig I support, as the result of these researches, Kleinenberg's view of the homology of the spinal ganglia of Vertebrates, and the parapodial ganglia of Annelids. But I go further, and say that what in the sense given above may be called the cranial neural ganglia of Vertebrates, are also morphologically equivalent to parapodial ganglia of Annelids. I also am fully prepared now to accept with Eisig the homology of the branchial sense organs of Vertebrates with the Seitenorgane of Annelida; but from the nature of the case it will be obvious that at present I cannot admit the unproved homology of the "Seitenorganen" ganglia of Annelids with the entire parapodial ganglia of Annelids. To meet the conditions of the Vertebrate head the parapodial ganglion must at some time or other have divided into two parts, one remaining neural and corresponding to the neural ganglia of Vertebrates, and one becoming lateral above the gill-clefts (and connected with them), which would correspond to the lateral sense-organ ganglia of Vertebrates, and to the same ganglia of Annelids. At present such a view would be merely speculative.

VIII. The Functional Distribution of the Cranial Nerves.

The recent researches of Gaskell (No. 19 *a*, p. 58) lead him to divide the anterior and posterior roots of each spinal nerve into two sets of fibres, which are visceral and somatic respectively.

Somatic motor nerves are those fibres derived from the anterior horn; somatic sensory nerves are those derived from the posterior horn; while the motor visceral nerves arise in the lateral horn and pass out with the other motor nerves in the anterior root; and the sensory visceral fibres take their origin in Clark's column and pass out with the posterior root.

Both sets of sensory fibres possess ganglia, the motor fibres being unganglionated.

I do not propose to devote any great amount of space to the examination of the bearings of Dr. Gaskell's results on the cranial nerves as given by himself, or as they appear to me; still, a few morphological conclusions can be drawn from those researches just as my results may be of use to the physiologist. The oculomotorius, trochlearis and abducens correspond morphologically and physiologically, as van Wijhe (No. 61), Hill (26), Gaskell (19),[1] and His (34) have insisted, to the motor somatic roots of spinal nerves. They arise in the combination of the anterior horn in the head, and they are distributed to muscles of the somatic system. Thus one is faced at once by the conclusion that the motor visceral fibres do not enter anterior roots in the head, and, on the contrary, they pass through the posterior roots, which are mainly sensory.

Now, these motor somatic fibres in the trunk develop as direct outgrowths of the spinal cord, and as the ganglia which form them lie in the cord they ought also to arise in the head as direct outgrowths of cells in the brain, and in the homologies of anterior root of spinal nerves. The latter is certainly not the case, for they pass out with the posterior roots: and the question arises, How do they develop in the head? Either the old course with anterior roots in the head never existed, or it has been lost, and they have acquired new paths through the afferent fibres of the posterior root.

Which of these things is really the case I cannot decide, for as yet I have been unable to prove the first by the demonstration of an element of the posterior root of a cranial nerve which develops as a direct outgrowth of cells from the brain.

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[1] Gaskell has quite recently arrived at very different conclusions ('Proc. Roy. Soc.,' Feb. 9th, 1888), which appear to be largely erroneous. I shall consider them in the second part of this work, after Dr. Gaskell has published the complete paper.

From what is known about the development of all other motor nerves, we may expect that such is the case; and I believe that sooner or later it will be shown that these fibres, which are the nerves to the muscles of the gill-clefts, do develop as direct outgrowths of cells in the brain like the anterior roots of spinal nerves.

When one also considers that to those four groups of nerves distinguished by Gaskell there must be added a fifth ganglionated sensory element connected with the lateral sense organs, the exceedingly complicated nature of the problems presented by the cranial nerves of any Vertebrate higher than Amphioxus will be very evident.

RÉSUMÉ OF RESULTS.

The spinal ganglia of Vertebrates are formed as differentiations of the inner layers of the epiblast just outside the limits of the neural plate. As the result of the cutting out from the epiblast of these ganglionic elements an appearance is presented by the epiblast which is left, to which Professor His gave the name of "Zwischenstrang." This has no share in the formation of the ganglia. "The Zwischenrinne" of His has no existence, but certain portions of the cranial ganglia, called here neural ganglia, are developed from the epiblast before closure of the neural tube in exactly the same way as the spinal ganglia. These portions of cranial ganglia are more or less homologous with spinal ganglia, possibly only with the sympathetic portion of the spinal ganglia Anlagen. After separation from the epiblast the neural cranial ganglia and the spinal ganglia get carried up with the closing in of the neural tube, and come to lie between its lips, but are quite distinct from the central nervous system, and the line of boundary between the two can always be distinguished. After the closure of the epiblastic folds the Anlagen grow out of their position between the lips of neural tube, which then also closes. They grow downwards and to the sides of the neural tube, and acquire their first and only connection with it by the probable growth of fibres from the ganglia into the central nervous system. The neural cranial ganglia also grow towards the lateral epiblast at the level of the notochord and fuse with it. Here are the Anlagen of the lateral or branchial sense organs of Froriep and myself. From this fusion in all Vertebrates form-elements pass into the cranial ganglia; these form-elements I distinguish as lateral ganglia. The parapodial ganglia of Annelids appear to be homologous with the spinal ganglia of Vertebrates, as Kleinenberg suggested, and also more or less with the neural cranial ganglia.

The anterior roots of cranial and spinal nerves arise as outgrowths of ganglia situate in the central nervous system. To form them cells leave the nervous system, and are distributed in the nerve. All the anterior roots at first contain many nuclei, which are of nervous and not parablastic origin. These statements on the anterior roots are only a confirmation of Balfour's researches.

In addition to the four elements of the anterior and posterior roots, two ganglionated and sensory, two motor and unganglionated, distinguished by Gaskell, Hill, and partially by His, the cranial nerves contain a fifth element, derived from the lateral or branchial sense organs. Such are, in very brief form, the main results of the researches recorded in the preceding paper.

It is with more than ordinary feelings that I desire to record here my most heartfelt gratitude to Professor Wiedersheim, in whose laboratory I carried out the above researches, for the generosity and kindness with which he in many ways supported my work. I owe him many thanks for his advice and criticism, and for the use of his valuable library, and, not least, for the gift of various material which was of great use to me.

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DESCRIPTION OF PLATES XVI—XXI,

Illustrating the Memoir by Dr. Beard on "The Development of the Peripheral Nervous System of Vertebrates. Part I."

List of References.

1. *iii*, *v*, *vii*, &c. Olfactory, motoroculi, trigeminal, facial, &c., nerves. *a.* Anterior root. *al. c.* Alimentary canal. *au. o.* Auditory organ. *br.* Brain. *br. gl.* Branchial or lateral ganglion. *cl.* Cleft. *e.* Epiblast. *f. br.* fore-brain. *f. gl.* Facial ganglion. *gl.* Ganglion. *gl. gl.* Glossopharyngeal. *g. A.* Ganglionic Anlage. *h. br.* Hind-brain. *h. c.* Head-cavity, or head-somite. *i. e.* Indifferent epiblast. *m.* Mesocephalic ganglion. *m. br.* Mid-brain. *me.* Mesoblast. *n.* Notochord. *n. s.* Nervous system. *olf.* Olfactory. *p. g.* Parapodial ganglion. *s. e.* Neuroepithelium. *sp.* Spinal. *sp. c.* Spinal cord.

All figures, except Fig. 64, are drawn under Zeiss's camera lucida. The magnification is indicated by such letters as Z. D, oc. 2, which signifies Zeiss's objective D, ocular No. 2. The objectives used were those of Zeiss and Hartnack, and are distinguished as Z. and H. respectively. Except Figs. 90—93, 96, 100, 101, which are from longitudinal frontal sections, the figures represent transverse sections.

All figures are reduced in the plates to two-thirds of their original size.

PLATE XVI.

Figs. 1—3.—Sections through the trunk of a Torpedo embryo. Z. D, oc. 2.

Fig. 4.—Section through the head region of Torpedo ocellata. Z. D, oc. 2.

Fig. 5.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Figs. 6 and 7.—Sections, head region, T. ocellata. Z. D, oc. 2.

Figs. 8 and 9.—Sections, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 10.—Section, mid-brain region, T. ocellata. Z. D, oc. 2.

Fig. 11.—Section, head region, T. ocellata. Z. D, oc. 2.

Fig. 12.—Section, head region, T. ocellata. Z. D, oc. 2.

Fig. 13.—Section, trunk region, T. ocellata. H. 8, oc. 2.

Fig. 14.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 15.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 16.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 17.—Section, trunk region, T. ocellata. H. 8, oc. 2.

Fig. 18.—Section, head region, T. ocellata. Z. D, oc. 2.

Figs. 19 and 20.—Sections, brain region, of two Torpedo embryos. Origin of olfactory neural ganglion. Z. D, oc. 2.

PLATE XVII.

Fig. 21.—Section through facial ganglion Anlage, T. ocellata. Z. D, oc. 2.

Fig. 22.—Section, trunk region, Mustelus lævis. Z. D, oc. 2.

Fig. 23.—Section, trunk region, M. lævis. Z. F, oc. 2.

Fig. 24.—Section, vagus ganglion, T. ocellata. Z. D, oc. 2.

Fig. 25.—Section, auditory organ and ganglion, T. ocellata. Z. D, oc. 2.

Fig. 26.—Section, spinal cord region, Pristiurus. Z. F, oc. 2.

Fig. 27.—Section, auditory region, T. ocellata. Z. F, oc. 2.

Fig. 28.—Section, trunk region, Pristiurus. Z. D, oc. 2.

Fig. 29.—Section, vagus region of head, T. ocellata. Z. D, oc. 2.

Fig. 30.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 31.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Figs. 32—36.—Sections, trunk region, Pristiurus. Z. D, oc. 2.

The order from before backwards is 33, 34, 35, 36, 32.

PLATE XVIII.

Fig. 37.—Section, anterior head region, T. ocellata. Z. C, oc. 2.

Fig. 37*a*.—The small figure marked out in preceding section under high power, to show Anlage of a cranial ganglion. Z. F, oc. 2.

Fig. 38.—Part of a section of head region, T. ocellata. Z. F, oc. 2.

Fig. 39.—Section, head region, T. ocellata. Z. F, oc. 2.

Figs. 40—42.—Portions of sections through head region of three Torpedo embryos. Z. F, oc. 2.

Fig. 43.—Section, trunk region, Mustelus. Z. D, oc. 2.

Fig. 44.—Portion of a section, trunk, T. ocellata. Z. F, oc. 2.

Fig. 45.—Portion of a section of Mustelus through vagus region. Z. F, oc. 2.

Fig. 46.—Section through auditory region of a Chick embryo. H. 9, oc. 2.

Fig. 47.—Section, head region, T. ocellata. Z. F, oc. 2.

Fig. 48.—Section, mid-brain region, Mustelus. Z. F, oc. 2.

Fig. 49.—Section, region of anus, Mustelus. Z. D, oc. 2.

Fig. 50.—Section, region of head, Mustelus. Z. C, oc. 2.

Fig. 51.—Section, trunk region, Chick, eight somites. Z. F, oc. 2.

PLATE XIX.

Fig. 52.—Section, anus region, T. ocellata. Z. D, oc. 2.

Fig. 53.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 54.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 55.—Section, trunk region, Chick, eight somites. Z. F, oc. 2.

Fig. 56.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 57.—Section, spinal cord region, Scyllium canicula. The epiblast is not represented. Z. D, oc. 2.

Fig. 58.—Section through developing anterior root of a spinal nerve, Mustelus. Z. F, oc. 2.

Fig. 59.—Section through tail region, T. ocellata. H. 8, oc. 2.

Fig. 60.—Section of developing anterior root (near anus), Mustelus. Z. D, oc. 2.

Fig. 61.—Section through trunk region, T. ocellata. Z. D, oc. 2.

Fig. 62.—Section, head region, Chick with no somites. Z. D, oc. 2.

Fig. 63.—Section in region of infundibulum, Chick, nine somites. Z. D, oc. 2.

Fig. 64.—Copy of Kleinenberg's figure of developing parapodial ganglion (*p. g.*) of Lopadorynchus. The sketch has been turned through 180 degrees.

Figs. 65 and 66.—Section, head region, Chick embryo with nine somites.

Fig. 67.—Section, head region, Chick embryo with four somites. Z. D, oc. 2.

Figs. 68 and 69.—Two sections through trunk and head regions respectively of a Chick embryo with four somites. Z. D, oc. 2.

PLATE XX.

All the figures on this Plate are from Chick embryos. All are under Zeiss's D, oc. 2.

Figs. 70—76.—Series of sections through trunk region, from behind forwards, of an embryo with six somites.

Figs. 77—79.—Series of sections from before backwards through brain region of an embryo with nine somites.

Fig. 80.—From same embryo, but through first somite.

Fig. 81.—From same embryo, but through end of second somite.

Figs. 82—84.—Three sections through brain region of an embryo with seven somites.

Fig. 85.—Section through spinal region of same embryo.

Figs. 86 and 87.—Two sections through brain region of two embryos with no somites.

Fig. 88.—Section, hind-brain region of a Chick embryo with ten somites.

Fig. 89.—Section, trunk region of a Chick with eight somites.

PLATE XXI.

Figs. 90 and 91.—Two longitudinal frontal sections through the head of a three-days' Chick embryo, showing the rudiments of branchial sense organs. Z. A, oc. 2.

m = Mesocephalic ganglion and sense organ.
v. Trigeminus ,, ,,
vii. Facial ,, ,,
ix. Glossopharyngeal ,, ,,

Fig. 92.—Trigeminus ganglion and sense organ from Fig. 91, highly magnified. Z. F, oc. 2.

Fig. 93.—Mesocephalic ganglion and its sense organ from Fig. 91, highly magnified. Z. F, oc. 2.

Fig. 94.—Section in front of a gill-cleft of T. ocellata. Z. A, oc. 2.

Fig. 94*a*.—The black portion of this section highly magnified to show growth and extension of the lateral sense-organ epithelium.

Fig. 95.—Section behind a gill-cleft of T. ocellata. Z. A, oc. 2.

Fig. 95*a*.—The blackened portion of this section highly magnified, to show growth and extension of lateral sense-organ epithelium. Some cells wander into mesoblast to form ganglion-cells.

Fig. 96.—Glossopharyngeal ganglion and its sense organ in three-days' Chick, from Fig. 90. Z. C, oc. 2.

Fig. 97.—Section of hind-brain of a Chick embryo with nine somites, showing "Zwischenstrang" (*Z.*) and its relation to ganglion Anlage, Z. F, oc. 2.

Figs. 98 and 99.—Sections of trunk region of Chick embryo of second day. Z. F, oc. 2.

Fig. 100.—Portion of longitudinal vertical section of mid-brain of a lizard embryo (L. agilis), showing origin of oculomotorius and its "ganglion" in brain. Z. D, oc. 2.

Fig. 101.—Portion of longitudinal vertical section of the auditory epithelium of a lizard embryo (L. agilis). Z. F, oc. 2.

Fig. 102.—Section, trunk region of a Chick embryo of second day. Z. F, oc. 2.

Fig. 103.—Section through glossopharyngeus nerve and ganglion of an advanced Torpedo ocellata embryo. Z. C, oc. 2.

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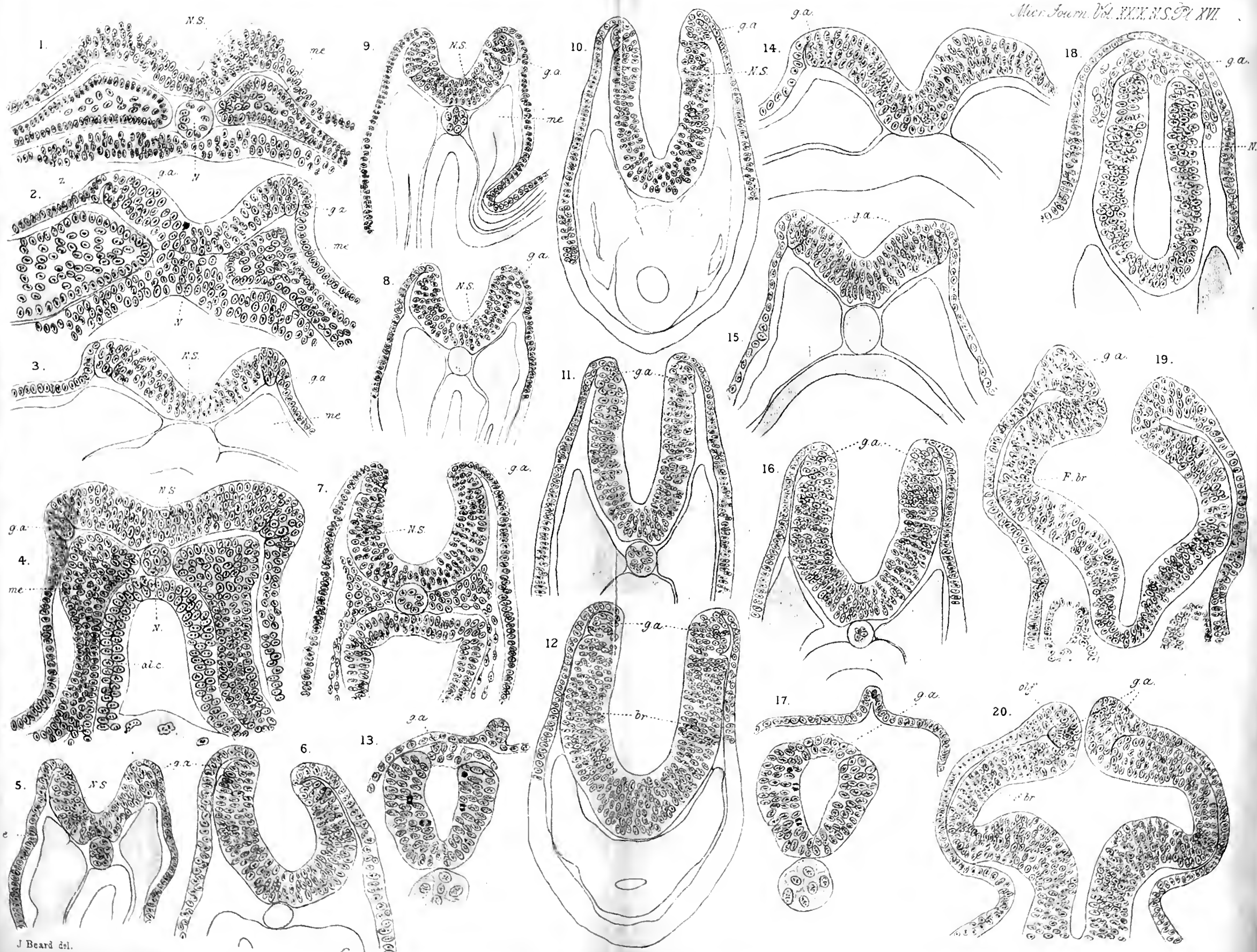

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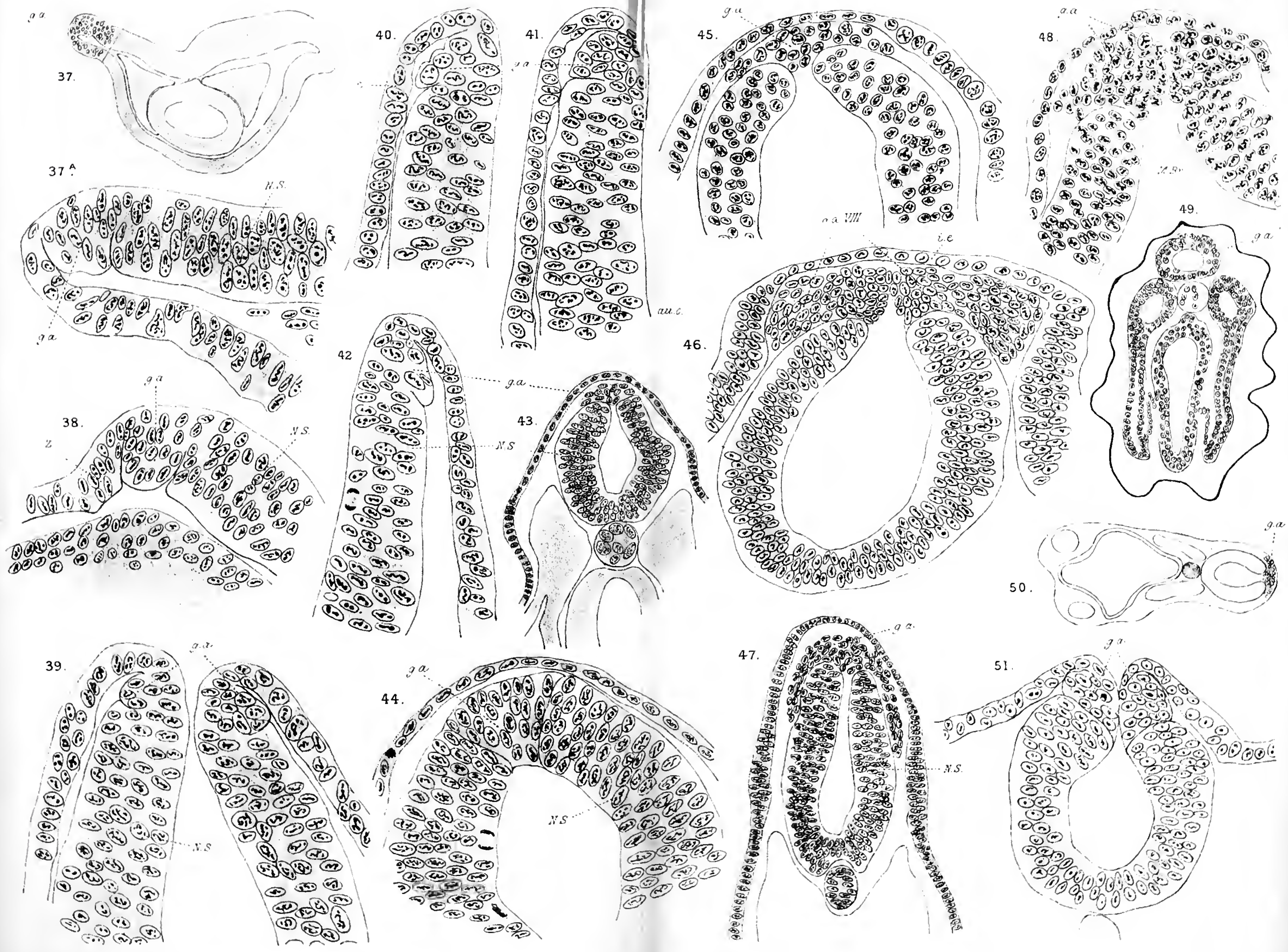
F Huth, Lith^r Edin^r

TORPEDO. OCELLATA.



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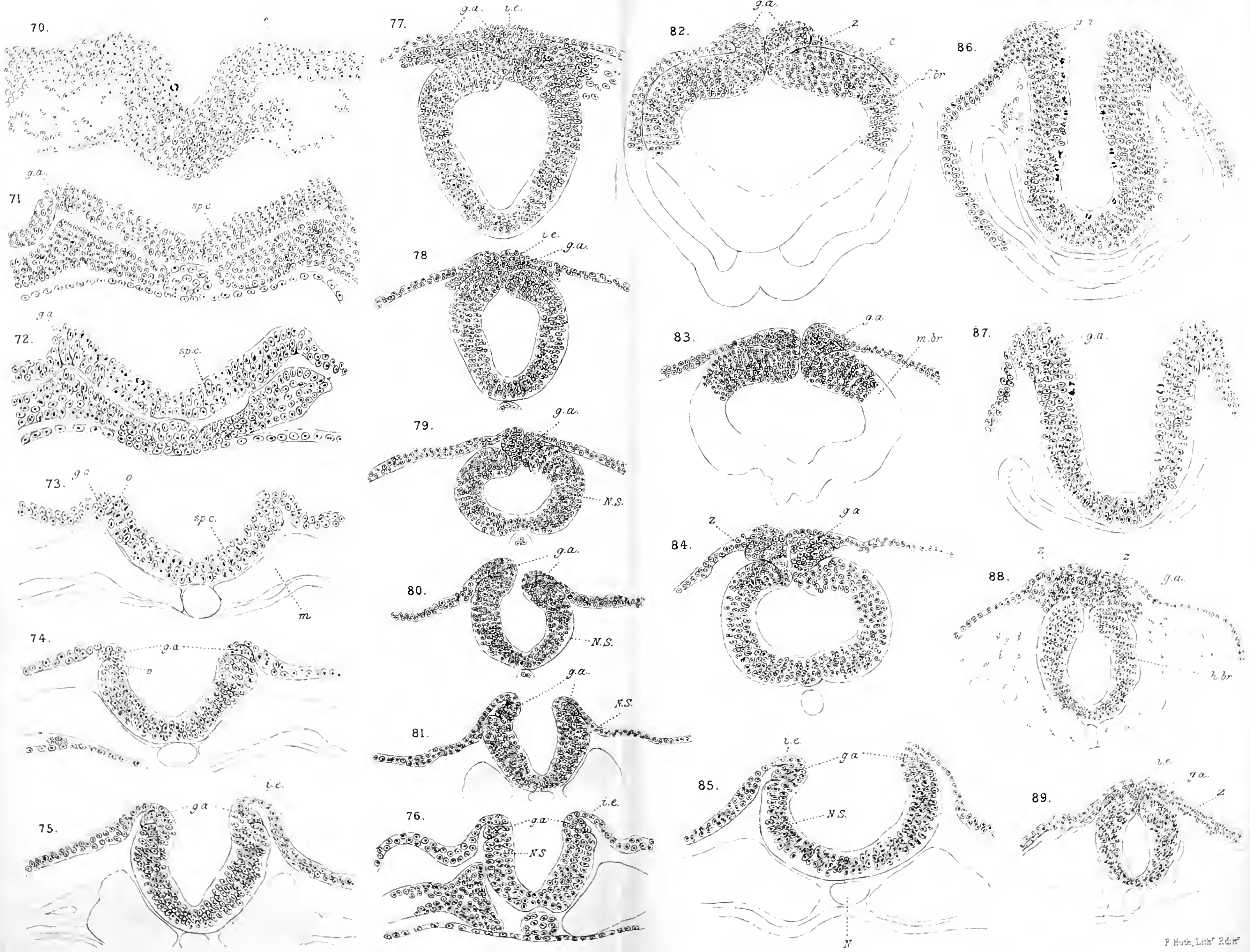
Fig^s 37–45 ELASMOBRANCHII. Fig^s 46–51 CHICK.



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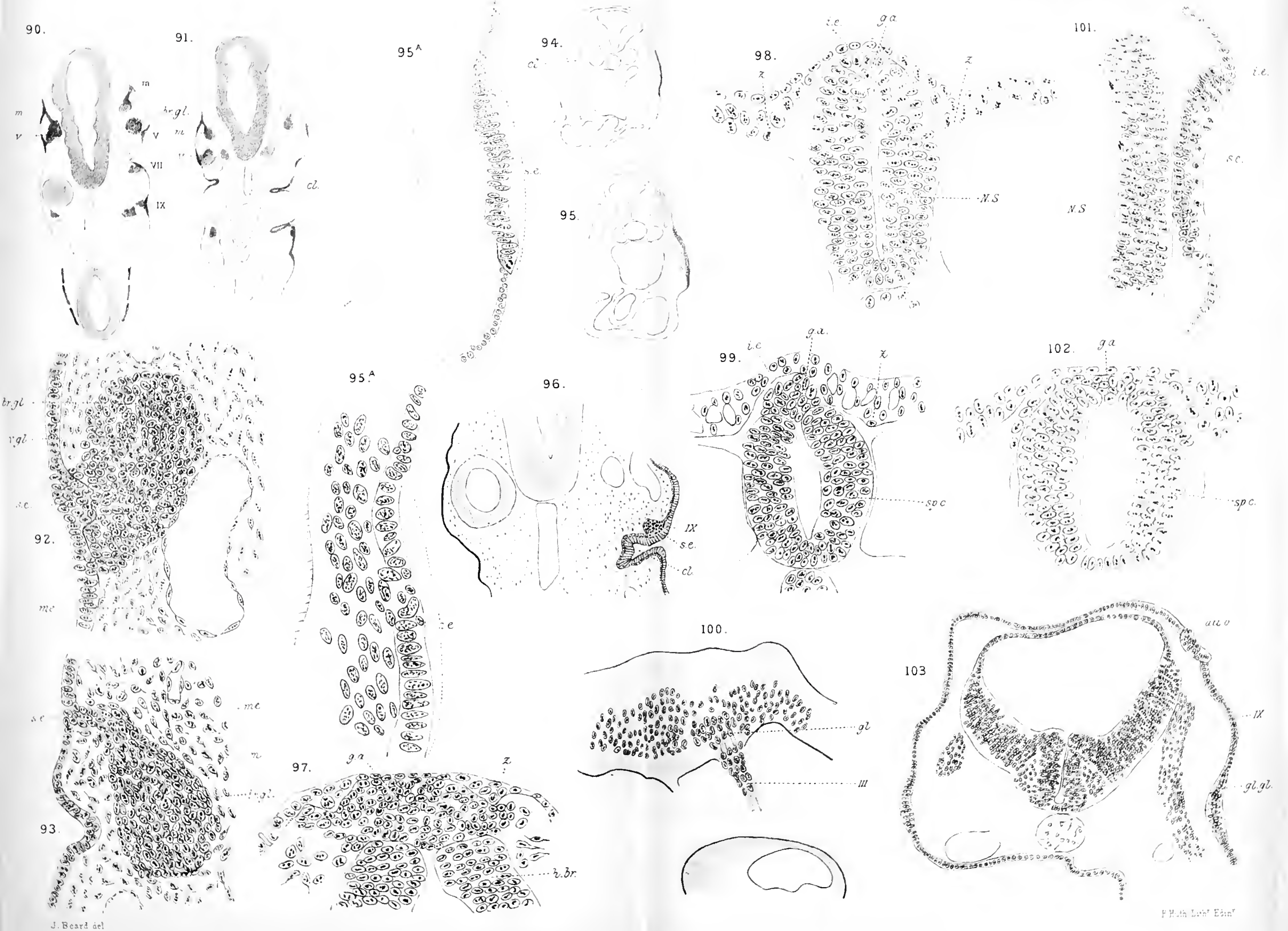
All the Figures are from CHICK EMBRYOS.



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Fig^s 90-93, 96-99, 102 CHICK. Fig^s 94-95^A, 103 T. OCELLATA. Fig^s 100,101 LACUTA.

Fig. 2.

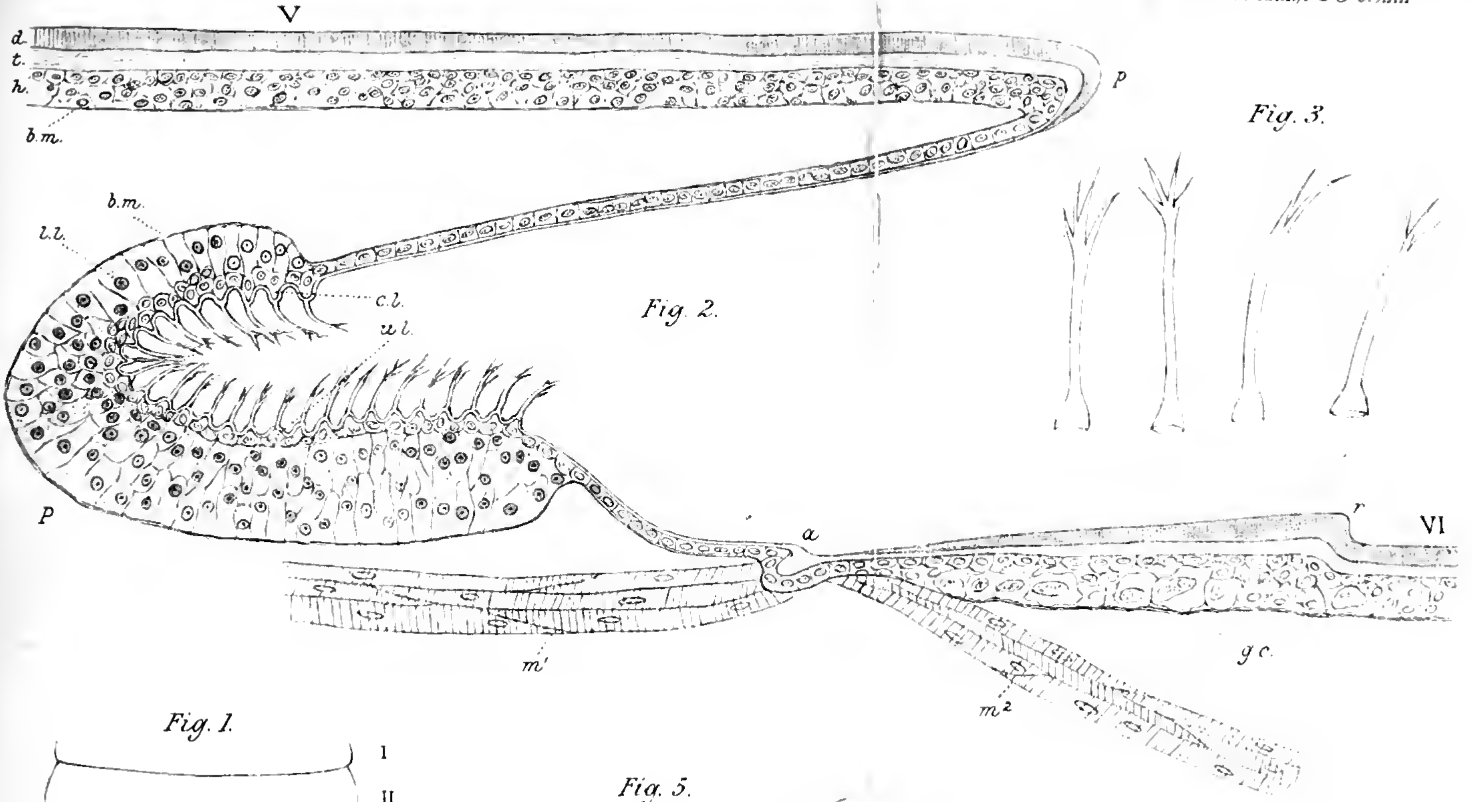


Fig. 3.

Fig. 1.

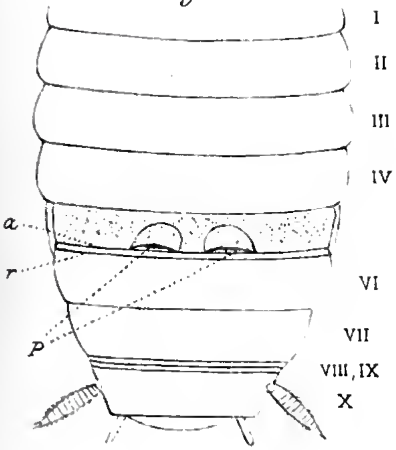


Fig. 5.

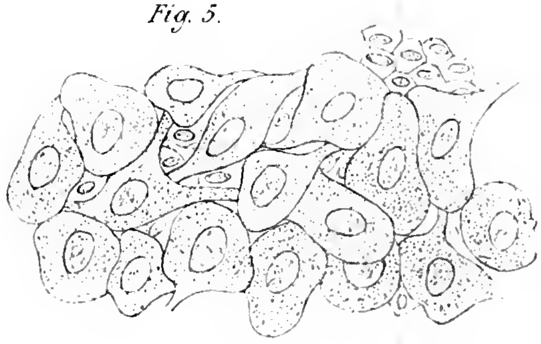


Fig. 6.

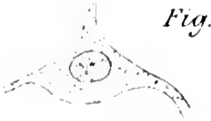


Fig. 7.

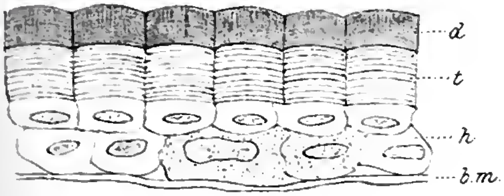
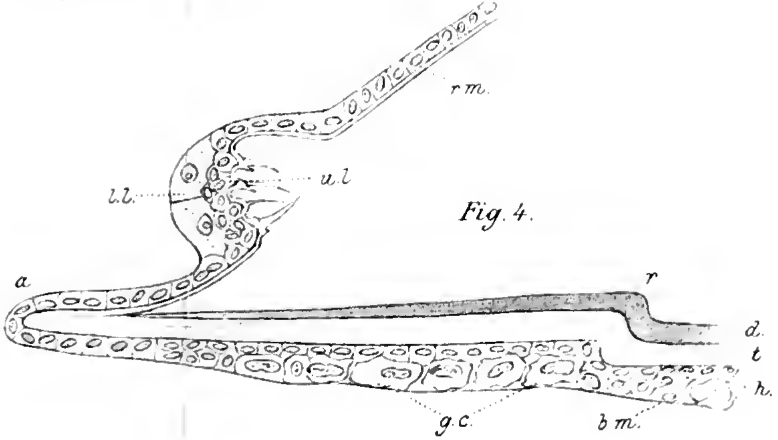


Fig. 4.



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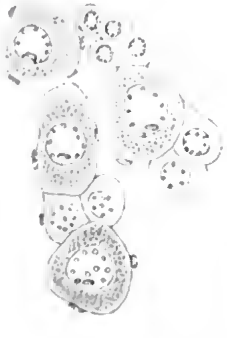

Fig. 3

Fig. 1.

Fig. 4.

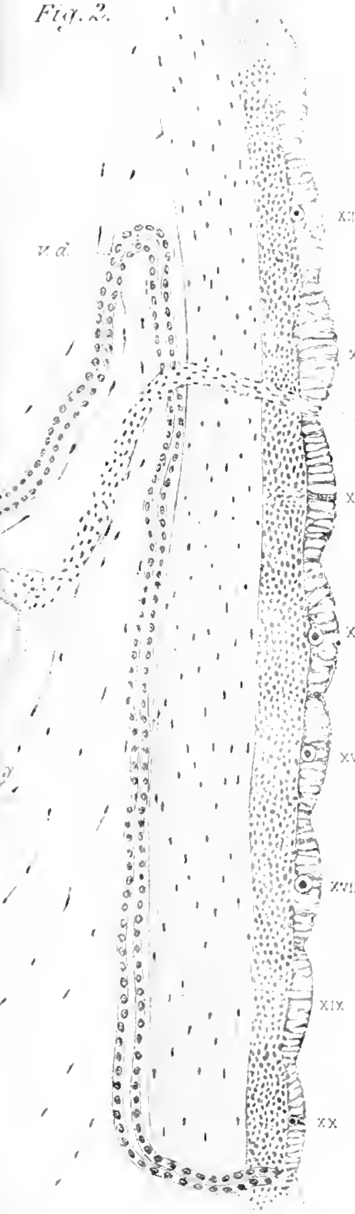

Fig. 2.

Fig. 6.

Fig. 5

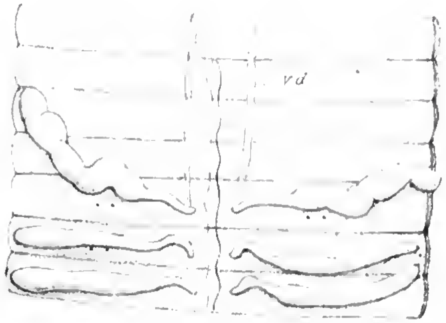

Fig. 7.

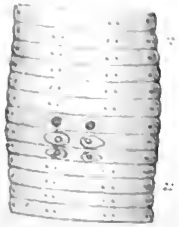

Fig. 8

Fig. 9.

Fig. 10.

Fig. 11.

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Note on a New Organ, and on the Structure of the Hypodermis, in Periplaneta Orientalis.

By

Edward A. Minchin,
Keble College, Oxford.

With Plate XXII.

The organ which I have to describe, and of which I have been unable to find an account in the latest works on the anatomy of the Cockroach, consists of two pouch-like invaginations of the cuticle lying close on each side of the middle line, between the fifth and sixth terga of the dorsal surface of the abdomen. In the normal condition these are covered by the fifth tergum, but when this is removed they are seen as two shallow pouches lying beneath the transparent intertergal membrane and opening to the exterior by two slit-shaped openings, which face backwards (fig. 1). They are lined by a continuation of the chitinous cuticle, which forms within the pouches numerous stiff, branched, finely-pointed hairs, beneath which, i. e. on the side towards the body-cavity, are numerous glandular epithelial cells. Fig. 2 shows a section longitudinal to the body of the animal passing through one of the pouches. The figs. v and vi are placed above the fifth and sixth terga respectively; *d.* denotes the upper dark layer, and *t.* the lower transparent layer of the chitinous cuticle, and *h.* the hypodermis of at least two layers, and resting on the basement membrane (*b. m.*). At *p.*, the most posterior point of the fifth tergum, the transparent layer of the cuticle and the uppermost layer of the cells of the hypodermis are continued into the intertergal membrane (*i. m.*), which again becomes continuous with the tergum immediately behind, the whole forming a continuous chitinous investment. The letter *a.*, figs. 1 and 2, denotes the most anterior extremity of the sixth tergum, to which the longitudinal tergal muscles (*m.* 1 and *m.* 2) are attached; *r.* is a ridge close behind this part, the space between *a.* and *r.* being usually overlapped by the hinder part of the fifth tergum. These parts are present between every pair of terga, but between the fifth and sixth are found in addition the peculiar glandular pouches (*P.*, figs. 1 and 2) above mentioned. As may be seen, they are lined by a cuticle continuous with that of the intertergal membrane (*c. l.*), which is produced into numerous stiff hairs, which bend towards the opening of the pouch. Below this cuticle is a layer of small flattened cells, with somewhat irregularly-shaped nuclei; this layer is evidently continuous with the hypodermic layer beneath the intertergal membrane (figs. 2 and 4, *u. l.*). These cells are crowded very close together, and their outlines are very hard to make out. Beneath this layer again comes a number of columnar cells with very distinct outlines, forming one layer on the dorsal side, and two or more on the ventral side of the pouch (*l. l.*). These cells have large rounded nuclei, each with a distinct nucleolus, and their cell contents are very granular. Outside all is a basement membrane continuous with that of the hypodermis. The tergal muscles pass immediately under the pouch, but I have satisfied myself, both by sections and by dissecting carefully, that the pouches have no special muscles. In fig. 3 are shown some of the hairs highly magnified. They are hollow and swollen at the base, and in a chloride of gold preparation processes of the cells of the upper layer (*u. l.*) can be seen running into them from below; sometimes nuclei are to be seen inside the swollen base. These hairs exactly resemble those found lining the abdominal stigmata, which are branched in exactly the same manner. Their chitinous nature is evident from the fact that if one of the pouches be macerated for a sufficient time in caustic potash (30 per cent.) nothing is left but the hairs and the cuticle on which they stand.

It is clear from the above description that these pouches are merely invaginations of the body wall between the terga, round which the hypodermis has greatly proliferated, and this is borne out by their development. Fig. 4 represents a section from a larva of about 8 mm. in length; there is a slight depression lined by a few chitinous hairs, which are branched at the base, and the cells of the upper layer are somewhat crowded. There are only two of the large columnar cells to be seen (*l. l.*), which are here rounded, and probably become columnar by flattening against one another. A series of gradations can easily be made out between this early stage and the adult stage shown in fig. 2. The fact of the hairs being branched at the base, and the crowding of the upper layer, seems to indicate that the hairs develop as simple foldings of the cuticle. The lower columnar cells seem to be modified hypodermic cells, but it should be noticed that they have a distinct nucleolus, which I have been unable to make out in other hypodermic cells; in fact their nuclei exactly resemble in shape, size, and appearance those of the fat-bodies.

As to the function of this organ, I have no doubt that it is glandular, and it is probable that it is a stink-gland, though I have not been able to satisfy myself of this. The interior of each pouch is usually filled with granular matter, which stains with hæmatoxylin but not with borax carmine. I have no doubt this is the secretion. The function of the hairs, into which the secretion must in the first place pass, may perhaps be to act as ducts, and at the same time to diffuse the odour by offering a larger surface for evaporation.

Structure of the Hypodermis.—Miall and Denny, in their valuable work on 'the Cockroach,' describe the hypodermis as a single layer of cells, each cell corresponding to a polygonal area of the chitinous cuticle, and resting on a basement membrane. Below this are described here and there large nerve-end cells which send up fine processes into sensory hairs on the upper surface. I am unable, however, to agree with this description as far as the dorsal surface is concerned. From my sections (see figs. 2 and 4) I find the hypodermis, in the older stages at all events, to consist here of two layers everywhere except where the cuticle is folded to form an articulation; in these parts only the upper layer remains. In certain places the cells of the lower layer become giant-cells (*g. c.*), which have large nuclei and very granular cell contents, and are provided with processes, and are without doubt ganglion-cells. They are scattered over each tergum, but are extremely abundant in the fore part of the tergum, i. e. that part which is overlapped by the tergum next in front, where they form an almost continuous layer. Hence it does not seem possible that they should always correspond with hairs. If a Cockroach be dissected in strong spirit, these cells can be seen with a low power forming irregular brownish patches in the fore part of each tergum, and with care they can be scraped off and floated on to a slide and stained and mounted in situ, when they present the appearance shown in fig. 5. They are large irregular cells, more or less overlapping one another and provided with processes, usually two or three. Between them are seen ordinary nucleated cells of the lower layer of the hypodermis, with which they are continuous. Fig. 6 shows a single one of these giant-cells. Though most numerous in the fore part of each tergum, they are also found scattered throughout its whole extent.

Hence I believe the hypodermis (fig. 7) to have the following structure: an upper regular layer of cells, which corresponds to the polygonal areas of the cuticle, and is continuous throughout the body, and is continued on to the tracheæ; and a lower, very irregular layer, which occasionally seems to form two layers, and is wanting where the cuticle is folded to form an articulation, and the cells of which are in places directly modified into nerve-end cells. These nerve-end cells are probably connected with a seta where the terga are exposed, but where they are overlapped seem merely to be connected with small papillæ. Below these two layers is placed the basement membrane (*b. m.*), which is apparently a thin, homogeneous membrane.

My investigations were carried on in the Morphological

Laboratory at Oxford, and in conclusion I have to express my thanks to Dr. S. J. Hickson, Mr. G. C. Bourne, and my tutor, Mr. E. B. Poulton, for much kind help and advice.

EXPLANATION OF PLATE XXII,

Illustrating Mr. Edward A. Minchin's paper "Note on a New Organ, and on the Structure of the Hypodermis, in Periplaneta orientalis."

Letters of Reference.

I—X. The ten terga of the abdomen. *P.* The glandular pouches. *a.* The anterior extremity of the sixth tergum. *r.* The transverse ridge across the sixth tergum, marking the part of it overlapped by the fifth tergum. *d.* The dark chitinous layer of the cuticle. *t.* The transparent ditto. *h.* The hypodermis. *b. m.* The basement membrane of the hypodermis. *p.* The posterior extremity of the fifth tergum. *c. l.* Chitinous lining of the gland. *u. l.* Upper layer of small cells of ditto. *l. l.* The lower layer of columnar cells of ditto. *m.* 1 and *m.* 2. Tergal muscles. *g. c.* Large ganglion-cells of the lower layer of the hypodermis. *i. m.* Intertergal membrane.

Fig. 1.—A diagram of the dorsal surface of the abdomen of the ♂ Cockroach, the fifth tergum being removed to show the two glandular pouches placed under the intertergal membrane between the fifth and sixth terga, which is represented dotted.

Fig. 2.—A longitudinal section through the adjacent parts of the fifth and sixth terga of an adult Cockroach, somewhat diagrammatic.

Fig. 3.—Some of the chitinous hairs lining the glands, highly magnified.

Fig. 4.—Longitudinal section through a gland of a larva of about 8 mm. in length.

Fig. 5.—Ganglion-cells of lower layer of hypodermis, mounted in situ.

Fig. 6.—Single ganglion-cell of lower layer of hypodermis.

Fig. 7.—Ideal section of hypodermis and cuticle.

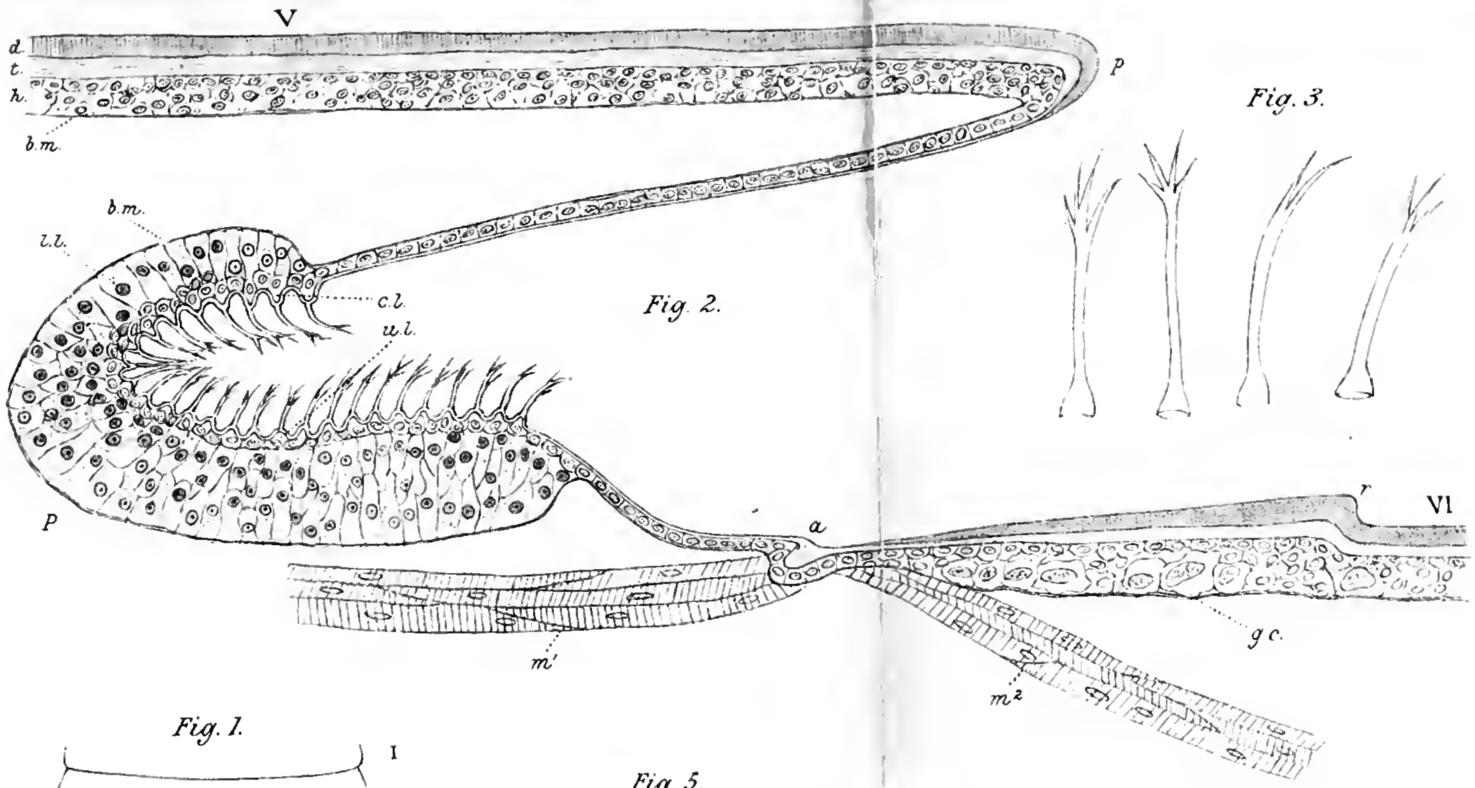

Fig. 2.

Fig. 3.

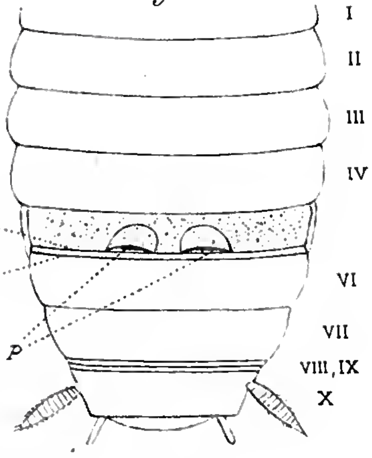

Fig. 1.

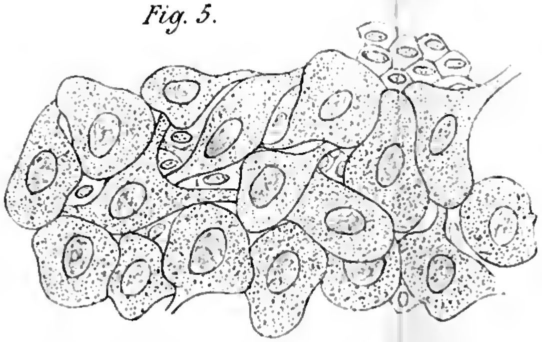

Fig. 5.

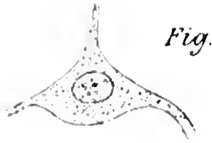

Fig. 6.

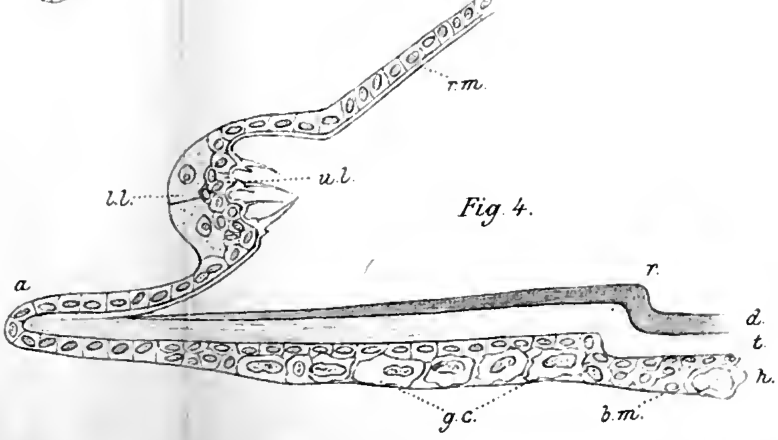

Fig. 4.

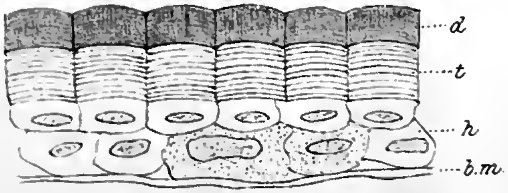

Fig. 7.

E.A. Minchin del.

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On Certain Points in the Structure of Urochæta, E. P., and Dichogaster, nov. gen., with further Remarks on the Nephridia of Earthworms.

By

Frank E. Beddard, M.A.,
Prosector to the Zoological Society of London, and Lecturer on Biology at Guy's Hospital.

With Plates XXIII and XXIV.

I. THE STRUCTURE OF UROCHÆTA.

M. PERRIER's elaborate memoir (22[1]) upon the structure of this worm leaves little to be done in the way of general anatomy. All the principal points which are of importance in the systematic grouping of Earthworms are thoroughly described and figured, with the sole exception of the female reproductive apparatus, which was not present in the examples studied by him. Perrier has also given a most detailed description of the vascular system down to the minutest ramifications, which forms one of the most complete accounts extant of the Annelid circulatory organs. The method of study adopted by M. Perrier was almost entirely that of laborious dissection, and the results which he has obtained by this means are undoubtedly striking. The elucidation of many points in the anatomy of Earthworms demands, however, a recourse to the section-cutting method, which has been adopted by myself in studying this Earthworm. I have, therefore, been able to add some few facts to what is already known, thanks to Perrier's researches, of the anatomy and histology of Urochæta.

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[1] The numbers enclosed in brackets refer to the "List of Memoirs" on pp. 279, 280.

§ Integument.

I have elsewhere (4) criticised Perrier's figures of the epidermis, and have now to make some remarks upon the penetration of blood-capillaries into the epidermis.

The vascularity of the epidermis in Annelids was first made known by Lankester (19) in Hirudo; subsequently Bourne (12) showed that in all the Gnathobdellidæ the epidermis was traversed by blood-capillaries. Claparède (13), and later Horst (17) and v. Mojsisovics (21), figured blood-capillaries in the clitellum of Lumbricus, but did not find them in the general epidermis. The first record of the presence of intra-epidermic blood-capillaries in an Earthworm is by myself (5) in Megascolex; subsequently (6) I found the same thing in Perichæta and Perionyx. The figures of Vejdovsky (29), Rosa (25), and Benham (9, No. 3) show that the epidermis of Criodrilus is also vascular. I have now to state that in Urochæta blood-capillaries penetrate between the cells of the epidermis. In the Leeches and in Criodrilus the blood-capillaries form loops in the epidermis, but in Urochæta I could never trace a returning limb of the capillary which entered the epidermis. Judging from Vejdovsky's figures (pl. viii, figs. 16, 17) of Limnodrilus, the blood-capillaries which enter the epidermis of that worm appear to end abruptly in the same way.

Quite recently the brothers Sarasin (27) have described the penetration of blood-capillaries into the epidermis of Perichæta (without referring, I may remark, to my own record of this fact, which may, however, have been inaccessible), which they furthermore observed to open on to the surface of the body, thus putting the blood-vascular system into communication with the exterior. This, if true, is a most remarkable fact. I cannot, however, pending the publication of their more detailed account, accept it. The blood-capillaries of Urochæta reach to the very cuticle, but there they stop. Furthermore, the following appears to be an argument against the free communication of the integumental blood-capillaries with the surrounding medium. These capillaries were perfectly obvious since they were gorged with blood; asuming for the present that they open by means of pores, it would no doubt be the case, as the Sarasins suggest, that capillary attraction would prevent the blood from leaving the body. But when the body of the worm is contracted by the preservative fluid the blood would surely be driven out through the pores. Nor can it safely be said that the contraction of the epidermic cells would be sufficient to occlude the orifice of the blood-capillary; this would be forced open by hydrostatic pressure induced by the far more powerful contractions of the circular and longitudinal muscles. I cannot, therefore, believe that—in Urochæta at any rate—there are any pores which put the hæmal system into communication with the surrounding medium; and in the meantime their resemblance to the integumental blood-capillaries of Limnodrilus is worthy of note.

§ Excretory System.

The nephridial system of Urochæta has been partly described by Perrier (22); according to his account it consists of (1) a large gland, termed "glande à mucosité," occupying the first few segments of the body; (2) a series of "segmental organs," one pair to each segment; (3) a series of remarkable structures only developed in the posterior region of the body, where they are present to the number of a pair to each segment; they coexist in these segments with the ordinary nephridia. I shall consider severally these different organs, which together constitute the excretory system.

Mucous Gland.—The mucous gland is figured and described by Perrier as consisting of a tuft of long, much coiled glandular tubules, which ultimately unite and open on to the exterior by a long muscular duct. The orifices are situated upon the first segment, and are each surrounded by a group of muscular fibrils forming a sphincter. I have already (4) pointed out the presence of this sphincter, which Perrier was unable to definitely prove. Its presence is of course a point of similarity between the mucous gland and the more typical nephridia of the succeeding segments.

The structure of the glandular tubules is compared by Perrier with that of nephridia, and he rightly points out their resemblance, abandoning his earlier belief (24) that these glands were a part of the alimentary system. At the same time Perrier does not consider that their homology with nephridia is definitely proved.

It will be obvious from an inspection of Pl. XXIII, fig. 1, of this paper that the structure of the mucous gland is identical with that of the nephridia. It consists of rows of perforated cells enveloped in a peritoneal sheath, which are so far absolutely indistinguishable from the nephridia of the remaining segments of the body.

There is one point, however, to which Perrier has not directed attention in his memoir, and which conclusively proves that these mucous glands are nephridial; that is, the presence of cœlomic funnels agreeing in their structure with the funnels of the nephridia in the other segments of the body.

The "mucous glands" occupy the first six segments, which contain no nephridia of the normal type; these latter do not commence until after. It is therefore a matter of interest to inquire how far the "mucous glands" represent the missing nephridia. Do they, in fact, simply represent the hypertrophied first pair of nephridia, or are they formed by a fusion of all the nephridia typically present in the space which they occupy? The fact that the external apertures are single would seem to prove the truth of the former supposition. On the other hand, the mucous gland does not only differ from the typical nephridium by its branched character, but also by the presence of several cœlomic funnels.

In my preliminary notice (2) of the mucous gland I have, I now believe erroneously, stated that each gland has four or five funnels. In several instances I have good reason to believe that there are only three present. The funnels are of considerable size, and apparently of a somewhat horse-shoe-shaped form; hence in a continuous series of sections it is not difficult to mistake one funnel for two contiguous but separate funnels. The three funnels of each mucous gland are, however, so widely separated that no mistake of that kind could be made. At the same time I do not wish to state positively that there are only three present; and for the matter of that, the exact number does not appear to me to be of great importance unless it could be proved that each branch opens into the cœlom by a funnel. I shall presently show reasons for believing that this is not the case. Now, two of these funnels are situated at the distal extremity of the gland and correspond in their position to the fourth segment; the third funnel is more anterior in position and corresponds to the fifth segment, so far as one can judge in the absence of definite septa separating these segments. Although there is some appearance of correspondence to the segments in the arrangement of the ciliated funnels, yet it must be admitted that the ciliated funnels are not arranged in a regular, metameric fashion. Taking into consideration the facts (to be referred to more at length below) that the nephridia of some of the posterior segments are furnished with more than a single funnel, and the extent of the first pair of nephridia ("tubiparous glands") of certain Polychæta sedentaria, it is perhaps more likely that the mucous glands represent the nephridia of the first segment alone; on the other hand, there is nothing in the facts, as I read them, which is contrary to the supposition that the mucous gland represents the nephridia of all the segments which it occupies, and that the primitive condition is only shown, and that imperfectly, in the disposition of the ciliated funnels; the concentration of this portion of the nephridial system being due to its specialised function.

Then again, there is a third alternative. Supposing that the mucous gland is the nephridium of the first segment alone, is its branching to be considered as a remnant of what I have elsewhere (1) urged is the primitive condition of the Annelid nephridium, or is the branching, as Dr. Eisig would argue (15), secondary? This raises again the whole question of the derivation of the Annelid excretory system, to which Dr. Eisig's recently published Monograph upon the Capitellidæ is a most weighty contribution.

In the latter part of this paper (p. 260) I discuss some general questions relating to the nephridial system of Earthworms; but it will be convenient to treat here of the arguments which the structure of the mucous gland of Urochæta, and of some other genera, furnish for the derivation of these glands from a continuous network of tubules.

I have already stated that this gland in Urochæta communicates with the cœlom by three funnels; I am not quite certain whether there is not a fourth. In any case there seems to be no doubt that the number of branches is in excess of the number of ciliated funnels. Perrier's figure of the organ (22, pl. xvi, fig. 35) is, so far as I can ascertain, accurate, in that it indicates the convergence of a large number of nephridial tubules to form the long duct of the gland. I have reason, however, to believe that in some cases the tubules unite before their opening into the muscular duct; but this is not a matter of great importance. One of two things must therefore follow: either the tubules again unite before the ciliated funnels, thus forming a network, or a large number (the greater number) of the tubules end blindly without any cœlomic apertures. I can find no evidence of the truth of the first supposition, and must therefore come to the conclusion that the mucous gland is a branched nephridium, of which the greater number of branches end blindly, while a few open into the cœlom by ciliated funnels.

These facts would seem to show that the gland is in some respects degenerate; that it primitively possessed a larger number of ciliated funnels, the greater part of which have been lost. So far this is merely an assumption, which at any rate harmonises with the structure of the organ. Although the nephridia of Earthworms are richly supplied with blood-capillaries, it seems nearly certain (particularly from the investigations of Kühenthal) (20) that a good deal of the waste matter that is excreted by them is not extracted from the blood-capillaries by the cells of the nephridia, but is taken up by the funnels; the large granular peritoneal cells which clothe the intestinal blood-vessels play an important part in this process of elimination.

Now, the very differences between the mucous gland and the other nephridia suggest that it plays a different part in the economy of the animal. A suspicion that this was the case led M. Perrier to term it "glande à mucosité," although he had no evidence to bring forward of a positive nature; this supposition would account for the reduction of the ciliated funnels; the high development of the secreting part of the organ, and the presence of a large vesicle for the storage of the secretion, coupled with the reduction of the cœlomic apertures, is clearly in favour of the view that this gland secretes a substance which is used for some definite purpose.

I describe below (p. 258) the structure and relations of the anterior section of the nephridial system in Dichogaster. This worm has an anteriorly situated gland which resembles in many particulars the mucous gland of Urochæta. It consists of a tuft of highly convoluted tubules which have the same structure as nephridia; these tubules open by means of a wider duct; the segments (Nos. 1—3) occupied by this gland contain no other nephridia. The "mucous gland" of Dichogaster differs from that of Urochæta in certain important particulars; in the first place it has no cœlomic funnels; in the second place the duct opens, not on to the exterior of the body, as in Urochæta, but into the buccal cavity; thirdly, it appears to be formed by a single tube much coiled. Apart from these points of difference, the similarity between the two glands is so great that I cannot but regard them as homologous. The fact that the mucous gland of Dichogaster opens into the buccal cavity suggests that its function is analogous to that of a salivary gland; it may be at least admitted that its function is probably different from that of the nephridia in the remaining segments of the body. A comparison between the structure of the mucous gland in the two genera Dichogaster and Urochæta leads to the inference, firstly, that they are homologous, and secondly, that they present two stages in the evolution of the gland. The primitive characters are more completely retained in the mucous gland of Urochæta; it possesses funnels and opens on to the exterior of the body on the first segment; the reduction in the number of the funnels, correlated with the changed uses (?) of the gland, culminates in Dichogaster, where there are no ciliated funnels; at the same time the external aperture comes to be situated in the buccal cavity.

I have elsewhere (7) described a similar gland in Acanthodrilus novæ-zealandiæ which, like that of Dichogaster, opens into the buccal cavity. I could find no ciliated funnels. In this case, as in that of Dichogaster, I discovered (see p. 259) the ciliated funnels of the nephridia elsewhere, and their absence from the mucous gland rests upon observations which are therefore more to be trusted.

Benham (9, No. 2) has recorded a gland in Diachæta which occupies the same position and has the same general appearance as the mucous glands of the types already referred to. He states that it is not a branched gland, but consists only of a single much contorted tube.

In Acanthodrilus annectens (Beddard 8) there are a pair of anterior nephridia exactly like those of A. multiporus; and each opens in the same way into the buccal cavity. I cannot discover very much evidence of this gland being branched; but fig. 14 appears to show that branching of the tubules does occur, though apparently not to any great extent.

There is nothing in the facts so far which is contrary to Eisig's supposition that the branching of the nephridium, whether of the terminal (external apertures) or distal (cœlomic funnels) region, is secondary; on the other hand, these facts may be equally well interpreted on the view that we have here a rudiment of a primitive condition in which the nephridial system formed a continuous network, with many funnels and many external apertures in each segment.

I shall now bring forward further evidence of the truth of this latter view.

Perrier has referred to the presence in Perichæta of a mass of glandular tubes in the anterior segments; these were figured by him in P. Houlleti, and were at first erroneously regarded as connected with the alimentary canal. Later, they were correctly referred to the excretory system. M. Perrier remarks (**22**, p. 639) "that the segments (in Perichæta) which contain these glands are usually filled by a thick yellow secretion, which the animal evacuates when annoyed." This secretion must be expelled, M. Perrier thinks, by the dorsal pores, since he was unable to discover any excretory canal like that of Urochæta. Now, Urochæta is an extremely small worm, and an anatomist who has proved himself sufficiently skilful, as M. Perrier has done, to dissect out the minute duct of the "mucous gland," embedded as it is among the muscles of the pharynx, would hardly fail to trace the same duct, if it existed, in the comparatively large Perichæta. By the study of transverse and—which are perhaps better for this purpose—longitudinal sections, I can quite confirm Perrier's conclusion as to the absence of an excretory canal like that of Urochæta. I have, however, already (**1**) shown that the nephridia of these segments open on to the exterior by numerous pores, and that the nephridia of adjacent segments communicate through the septa; this at any rate applies to P. aspergillum. In the few first segments of the body of P. aspergillum (**1**) the nephridial system is enormously developed; all the cœlomic space available is closely packed with tubules. On dissection this part of the excretory system has, comparatively speaking, a solid appearance; through the rest of the body the nephridia are by no means so conspicuous, and, indeed, they require a microscope for their demonstration.

The massing of the nephridia in a few of the anterior segments and their apparently different function from the nephridia in other parts of the body (if one may so interpret M. Perrier's experiments), renders plausible a comparison of this part of the excretory system with the "mucous gland" of Urochæta. If this comparison be allowed the most important consequences follow; it would seem, in fact, as if the specialisation of this part of the nephridial system ultimately led to the concentration of the numerous excretory pores into one long duct; that in fact the branched mucous gland of Urochæta is traceable to the specialised nephridial mass of the anterior segments of Perichæta; the numerous external pores of the latter being replaced by the single aperture of Urochæta.

I have in a previously published paper pointed out that if the peculiar cutaneous glands of Urochæta correspond to abortive setæ, as they appear to do from a comparison with similar glands in Anachæta (Vejdovsky, **29**, pl. vii, fig. 1), the eight setæ per segment of Urochæta are brought about by a reduction of a complete circle of setæ such as exists in Perichæta. On this hypothesis Perichæta is the primitive form, Urochæta comes next, and finally Dichogaster and Acanthodrilus, in which there is no trace of the missing setæ, complete the series. It will be noticed that the evolution of the mucous gland, as I have traced it in the foregoing pages, is in correspondence with this series of facts.

Nephridia.—All the segments of the body in Urochæta from the fifth are furnished with a pair of nephridia.

The external apertures of these are perfectly plain on the exterior of the body.

Perrier has already referred to the fact that the aperture of the nephridium is surrounded by a peculiar cup-like structure, which seems to be composed of radially arranged, short muscular fibres. He has also figured the funnel. I find that with respect to the funnel there is a remarkable difference between the mucous gland and the nephridia of the anterior segments on the one hand and the posterior nephridia. Perrier's figure of the nephridial funnel (**22**, pl. xvi, fig. 42) evidently represents one of the latter. The funnels of the mucous gland of the nephridia of the anterior segments are in the first place much larger than those of the posterior nephridia; their structure also is different. The funnel itself (Pl. XXIII, fig. 5) is composed of the same columnar ciliated cells with large nuclei, but it does not at once communicate with the narrow tubule; the latter is dilated into a wide cavity of considerable length. This portion of the nephridium is not to be confounded with the funnel although its lumen is of the same size; its walls are tolerably thick and exhibit a faint transverse striation, and contain oval nuclei embedded at intervals. The structure of this part of the nephridium shows that the lumen, although it is extremely wide, is nevertheless intracellular; it is simply a dilatation of the tubule.

This dilatation of the nephridial tubule recalls an analogous dilatation which Bourne (12, figs. 51, 52, 53, 54), has described and figured in Leeches, only in these animals the lumen appears to be intercellular.

I have always observed this dilatation to be filled with what are apparently degenerating corpuscles, the nuclei of which were deeply stained by borax carmine. Bourne has observed similar contents in the corresponding part of the nephridium in Leeches.

In the genus Thamnodrilus (Beddard, 3) the funnels of the anterior nephridia also differ from the funnels of the posterior nephridia.

In a few segments I observed two nephridial funnels, but this branching of the nephridium appears to be rare.

Perrier states that the nephridial funnel is contained in the same segment as the nephridium itself. In a paper upon the structure of an Australian species of Urochæta (4) I pointed out that the funnel, as is usually the case among the Oligochæta, was situated in the segment anterior to that which is occupied by the rest of the nephridium. In Urochæta hystrix I find a justification for Perrier's statement; the nephridia are sometimes entirely contained in one segment and sometimes are not. In the second case the funnel is in the segment in front; the former arrangement seemed to be restricted to the anterior nephridia. Finally, the anterior nephridia agree with the mucous gland, and differ from the posterior nephridia in the small calibre of the duct; in this they agree with the anterior nephridia of Perichæta (see p. 262).

Ovaries and Oviducts.—Perrier's memoir (22) upon Urochæta contains no description of the female reproductive organs, except of the spermathecæ. He remarks "that the female reproductive apparatus seems to be fully developed after the male reproductive organs." This opinion is borne out by my own experience. I have never found the two sets of organs to be completely developed in the same individual. All the specimens that I have examined were either "males" or "females." This functional separation of the sexes, so frequent in hermaphrodite animals, cannot be said to be general among Earthworms. Benham, however, has found (9, No. 2) that Urobenus, Diachæta, and Trigaster agree with Urochæta in this particular; in the two first genera he could only discover the male organs, while in Trigaster the female organs alone were fully developed.

I have investigated the minute structure and the position of the generative organs, both by transverse and longitudinal sections; their position and general relations could only be properly determined by longitudinal sections, owing to the arrangement of the septa in this region of the body. Perrier has already recorded the fact that in the specially thickened septa—the last of which bounds the tenth segment—the middle region is very far behind the lateral margins which are attached to the parietes. Each septum is therefore somewhat thimble-shaped with the concavity forwards, and is largely enclosed by the following septum. This does not only apply to the thick septa, but to a large number of the excessively fine septa which come behind. It is not in fact until the twentieth segment that the intersegmental septum is disposed perpendicularly to the long axis of the body. The ovaries and oviducts are situated anteriorly where the delicate septa are hardly separable. The ovaries and oviducts, as well as the funnels of the vasa deferentia, come to lie opposite to the setæ of segments which in reality are considerably behind those which contain the several organs. In correspondence with the arrangement of the septa the oviducts run forward for some distance before opening on to the exterior. Their position, however, is in reality perfectly normal. The external apertures are upon the fourteenth segments, and the funnels open into the thirteenth.

The vasa deferentia funnels open into the segment in front, i. e. the twelfth.

In two specimens I found the female reproductive apparatus fully developed, and the male organs, with the exception of the vasa deferentia, not fully developed. The vesiculæ seminales in those individuals were very readily visible as outgrowths of the posterior side of the septum which separates segments 13 and 14; the vesicula was in the condition illustrated by Bergh (11) in Lumbricus on pl. xxi, fig. 13, of his memoir. It consisted for the most part of a solid mass of cells, with a narrow lumen extending for a very short way into its thickness.

In these specimens (Pl. XXIII, fig. 2) there were no testes, but the twelfth segment as well as the thirteenth contained a pair of ovaries. In another individual the gland of the thirteenth segment contained ova in abundance. There were also a few ova in the gland of the twelfth segment. I figure (Pl. XXIII, figs. 3, 4) a small fragment of the glands of segments 12 and 13. In another specimen in which the vesiculæ seminales were in a further advanced condition, the genital gland of the twelfth segment and that of the thirteenth segment appeared to be a testis. These facts are, of course, a confirmation (though indeed a confirmation is hardly wanted) of the accepted view that the ovaries and testes are serially homologous structures. From this point of view the facts are of just as great importance, even if it were shown that the individuals were only abnormal. I am inclined to believe, however, that they are not so, and that in Urochæta the same gland may produce ova or spermatozoa.

In all the four individuals which I investigated by means of longitudinal sections there were a number of bodies resembling mature ova lying in the body-cavity behind the thirteenth segment quite detached from the reproductive glands of that segment. They appeared to be contained in the fourteenth or fifteenth segment, or even to occupy both of these segments. In at any rate one instance these bodies appeared to be contained in a thin-walled muscular sac, to the walls of which were closely applied the transverse vascular trunks. In the other cases they were grouped together, but I did not observe any structure resembling a muscular sac surrounding them.

The maturation of the ova[1] of Urochæta outside the gland in which they are developed is of some interest, even if the supposed muscular sac enveloping them is nothing but a partially detached (by the processes of embedding, &c.) portion of the delicate intersegmental septa. Moreover, the ova themselves differ in some important particulars from the ova of the majority of Earthworms.

Vejdovsky (**29**), as well as the earlier observers d'Udekem and Claparède, dwells upon the fact that the ova of Earthworms are small and numerous as compared with those of the majority of the aquatic Oligochæta, which are large and few. The greater size of the ova of the "Limicolæ" is due to the fact that they contain very much more abundant yolk. The greater development of yolk in the ova of the "Limicolæ" is, Vejdovsky thinks, due to the different way in which they become mature. In the aquatic Oligochæta the ova detached from the ovary are nourished by the perienteric fluid, while the ova of Earthworms remaining in the ovary are provided with special blood-capillaries. The latter mode of nutrition, as the facts prove, leads to the formation of numerous small ova, the former to the

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[1] I found these structures in two specimens of Urochæta, and occupying the same position. I cannot, however, be certain that they are not Gregarines. I am not aware that it is possible in preserved specimens to be absolutely certain about such a point. All that can be said is that the bodies in question are closely similar to the ovarian ova of Phreoryctes, and that I only found them in the situation mentioned. The fact of their not being surrounded by smaller ovarian cells as are the egg masses of Rhynchelmis is not a conclusive argument, since in Earthworms the ova in the receptaculum are not accompanied by such cells.

increase in size of a few ova. Whatever may be the fundamental explanation of this structural dissimilarity, the fact remains that there is a certain difference in the mode of development of the ova in the aquatic and in the terrestrial Oligochæta. At the same time it has to be borne in mind that in many Earthworms the ova when fully developed leave the ovary and make their way to the interior of receptacula ovorum. These chambers must at least be analogous to, if not homologous with, the "egg-sacs" of Stylaria, &c., in which ova also undergo maturation. They differ, however, in being relatively much smaller and thicker walled, and in having their cavity divided up by trabeculæ like the vesiculæ seminales. Vejdovsky does not give a detailed account of the development of the egg-sacs (Eiersäcke) in Stylaria, and their homology with the receptacula ovorum of Earthworms must be left for the present undecided. The question as to homology does not, however, affect the functional similarity of the two structures. The receptacula ovorum of Earthworms are thicker walled, and supplied with abundant blood-capillaries, which give them a reddish appearance. The egg-sacs of Stylaria are thin walled, and have no capillary network, but are supplied by the hypertrophied vascular arch of their segment. This difference may perhaps be responsible for the unequal development of the contained ova in the two cases. The whole question requires further investigation.

Judging from Bergh's (11) figures, the mature ova contained in the ovary of Lumbricus hardly differ in size from those contained in the receptacula ovorum. I have carefully compared the relative sizes of the ovarian ova and those from the receptaculum ovorum in Allurus, and find that the latter are rather larger; but the difference is not sufficiently striking to lead me to the opinion that the ovum undergoes any important increase of bulk during its sojourn in the receptaculum. Indeed, the observations of Dr. A. Collin (14) show that in Criodrilus the ova contained in the receptaculum are smaller than the largest ovarian ova; but this is probably to be explained by supposing that the smaller immature ova ripen in the receptaculum, while the large mature ova pass from the ovary directly into the oviduct.

The mature ova of Allurus and perhaps of Urochæta differ from those of the majority of Earthworms, and agree with those of the "Limicolæ," in the fact that they are of comparatively large size.

The only other Earthworm known to me, in which the ova are of large size, is Allurus. Fig. 22 of Pl. XXIV illustrates the comparative size of the mature ova of a number of Earthworms and of Phreoryctes. It will be seen from that figure that the ova of Allurus are markedly larger than those of Eudrilus, &c., though smaller than the supposed ova of Urochæta. This fact is of particular interest in relation to other points in the structure and economy of Allurus. This worm, although structurally nearer to Allolobophora than to any other Oligochæt, is not terrestrial; at least, not exclusively terrestrial in its habits. I received some specimens from Teneriffe which were collected in company with a number of specimens of Lumbricus and Allolobophora in soil; on the other hand, Mr. Martin Woodward was so good as to forward me a specimen of Allurus, which he discovered in a vessel containing Chara which had been collected for the use of the botanical students at the School of Science, South Kensington. There was no reason to believe that this individual had accidentally found its way into the vessel; it had been in all probability collected in the stream which furnished the Chara. Mr. Benham has lately contributed to 'Nature' a note in which he points out that Allurus is largely aquatic in its habits.[1] It is interesting to find that this particular genus approximates to the "Limicolæ" in its habits; indeed, it is the only instance known to me of an aquatic Earthworm, though of course many of the "Limicolæ" live in damp soil.

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[1] Since writing the above I find that Vejdovsky in his paper upon Rhynchelmis ('Zeitschr. f. wiss. Zool.,' 1876) has mentioned the occurrence of Allurus in streams. During a recent visit to the Plymouth Station of the Marine Biological Association I found Allurus in abundance among coarse gravel in the River Plym, near Bickleigh.

Allurus, furthermore, resembles certain of the Limicolous genera in the large size of its ova, and in the fact that the female reproductive pores are behind the male. I have not any evidence that Urochæta can, like Allurus, lead an aquatic life; but the resemblance which it bears to the "Limicolæ" is shown in the possession of bifurcate setæ as well as (perhaps) in the large size of its ova. Perrier discovered the former fact, and I have occasionally observed the same in specimens from British Guiana.

II. Dichogaster Damonis, nov. gen. et sp.

The present section contains some account of the anatomy of a species of Earthworm, which appears to be sufficiently unlike any other type at present known to justify the creation of a new genus for its reception.

I have examined two specimens which I acquired from Mr. R. Damon, of Weymouth. One of these was dissected, the other studied by means of transverse sections.

The worms formed a part of the Godeffroy collection, recently purchased by Mr. Damon, and are labelled "Hypogæon." This name has been applied to several very different species of Earthworms, and in Savigny's original description is characterised by the possession of a single median seta in addition to the eight which are ordinarily found. In this character Hypogæon differs from the present species.

The species was collected in Fiji.

§ External Characters.

The setæ are paired, and lie on the ventral side (fig. 8). The dorsal and lateral pair of setæ are separated from each other by a rather greater interval than that which separates the ventralmost pairs of setæ. The clitellum extends from segments 13—20 inclusive. It is not so markedly developed on the ventral as on the dorsal side; hence the number of segments of which it is composed can be more easily reckoned from the ventral side. The twentieth segment has the whole ventral region enclosed between the lateral pairs of setæ entirely devoid of glandular epithelium, which is only developed on the dorsal region of this segment. The more anterior segments, in like manner, have no development of glandular substance for the greater part of the ventral area. The seventeenth segment bears the apertures of the vasa deferentia, which do not correspond to the ventral setæ, but are more ventrally placed. The apertures are situated on a tumid area which occupies the space lying between the setæ. On the two following segments there are similar areas, but more distinctly marked off from the surrounding integument. Dorsal pores are present, but I could not ascertain where they commenced.

On the eighth segment are the apertures of the single pair of spermathecæ. These are closely approximated in the median ventral line, and open near to the anterior margin, as is so generally the case. The various layers which compose the body wall appear to have much the same structure in this as in other species of worms. Particularly noteworthy is the fact that the longitudinal muscular layer shows the bipinnate arrangement of its fibres which is so characteristic of some, although not of all, species of Lumbricus, and is found also occasionally in other genera. This is illustrated in fig. 6 of Plate XXIII. In the anterior part of the body the fibres of the longitudinal muscular coat do not show any such regularity in their arrangement.

§ Alimentary Canal.

The most salient fact in the structure of the alimentary canal of this Earthworm is the presence of two gizzards (fig. 21); these are situated close together in consecutive segments, and are only separated by a very minute œsophageal portion, the calibre of which is not far short of that of the gizzards themselves; the segments occupied by the gizzards are 7—10, the mesenterics separating these segments from each other are, as is often the case, not obvious. It will be seen, therefore, that each gizzard occupies two segments. The presence of more than a single gizzard is not new among Earthworms; Digaster, Perrier (24), and Didymogaster, Fletcher (16), as their names imply, have two gizzards, but the present genus cannot be confounded with any of these; more than two gizzards occur in other Lumbricidæ, viz. Trigaster (Benham) and Moniligaster (Perrier).

The œsophagus is furnished behind the gizzard with calciferous glands; of these there are three pairs, situated in segments 15, 16, and 17 respectively (fig. 21); the two anterior pairs of these glands are rather larger than the posterior pair and in the specimen studied by me were full of calcareous particles, the product of their activity, which were entirely absent from the smaller pair; the œsophagus contained a large quantity of the calcareous secretion of the calciferous glands.

The posterior pair of calciferous glands is divided by longitudinal furrows into four distinct lobes; its blood supply is derived direct from the dorsal vessel, there being apparently no supra-intestinal trunk; the blood-vessel enters the gland along the short pedicle, which unites it with the walls of the œsophagus. The same appears to be the case with the two anterior pairs, and in all the glands the vascular supply is also in connection with the blood sinus of the œsophageal walls.

§ Generative Organs.

Testes and Vesiculæ Seminales.—I have only been able to study these structures by means of transverse sections; by dissection I could not, owing to the friable condition of the specimen, make out the exact relationship between the component parts of the male generative organs.

The testes (fig. 15, *t.*) are two pairs of small glands situated in segments 10 and 11. The organ is somewhat irregular in shape, and furnished with numerous finger-shaped processes. A dissection even of the immature example which I studied by transverse sections would not have shown the testes, inasmuch as they are completely overgrown and surrounded by the vesiculæ seminales of their respective segments.

The fact that the testes are actually surrounded by the vesiculæ during the growth of the latter is, of course, a result of numerous investigations. The adult structure of the Earthworm at present under consideration would prove this point, supposing, that is to say, that there was the least need of proof.

The sac-like vesiculæ seminales completely enclose the testes, and in the case of the anterior pair, at any rate, enclose also a tuft of nephridial tubules, which happen to be closely associated with the testes. In other worms other organs of the body, e. g. the ventral blood-vessel, are enclosed within the cavity of the vesiculæ.

The testes of Dichogaster have apparently the same structure that characterises these organs in other Earthworms. They are attached to the mesentery close to the ventral median line on either side of the nerve-cord ; at the point where they are attached the walls of the vesiculæ come into contact, and are fused with the mesentery.

The structure of the vesiculæ seminales is curious and differs in certain particulars from the vesiculæ of other Earthworms.

In the example which I dissected the eleventh and twelfth segments contained each a pair of racemose structures of small size (fig. 15, *r.'*), appearing on each side of the gut. These presented every resemblance to the vesiculæ seminales of many species of Acanthodrilus. In the tenth segment a mass of developing spermatozoa occupied the ventral region of the segment, and partly obscured the fimbriated apertures of the vasa deferentia. A study of the generative apparatus by means of transverse sections showed that the structure in segment 10 is not a loose mass of developing spermatozoa set free from the vesiculæ of segments 11 and 12, and ready to be extruded through the open funnels of the vasa deferentia. It is really a pair of vesiculæ seminales (fig. 15, *r.*) with a delicate outer wall, and presenting the usual structure. This vesicle, although presumably originally a paired structure, does not show much evidence of being a paired structure in the adult worm; the two halves of the vesicle are almost completely fused in the ventral median line where they enclose the nerve-cord. The ventral blood-vessel is not enclosed within the vesiculæ, but is suspended by a vertical mesentery some little way down between the two vesiculæ, which here become distinctly separate; a portion, however, of the transverse vessel of this segment, as well as (necessarily) a branch on each side, which runs to the testis, are enclosed by the vesiculæ. The vesiculæ send off a narrow lateral band, which seems to become fused with its fellow of the opposite side in the dorsal median line (see fig. 15).

In the eleventh segment is another pair of vesiculæ, for a description of which the foregoing remarks will nearly suffice. The same segment also contains (see fig. 15) the racemose structures already referred to. These are composed of a large number of small spherical acini, which contain bundles of developing spermatophora. The whole structure is firmly attached to the mesentery, which divides its segment from the one in front. I have not been able to make out any connection between this portion of the vesiculæ and the undivided median sac.

Finally, segment 12 contains another pair of these racemose organs, which have apparently no connection with the vesiculæ of the preceding segment.

Vasa Deferentia.—There are two pairs of vasa deferentia funnels situated in segments 10 and 11; they open into the middle of the vesiculæ seminales of these segments, on each side of the nerve-cord and near to it. Their structure calls for no special remark, neither does that of the vasa deferentia, which open, in common with the glandular body, upon the seventeenth segment of the body.

When the worm was opened in dissection the seventeenth, eighteenth, and nineteenth segments were seen to be largely occupied by three pairs of glands, a pair to each segment, of a whitish colour, and meeting above the intestine. The anterior pair of these is very much larger than those which follow, and somewhat contorted; the latter are narrower tubular organs exactly resembling each other (fig. 7).

An examination of these glands by transverse sections shows that they all open on to the exterior at a corresponding point in the three segments; the external apertures of these glands, in fact, correspond in position to the innermost of the ventral pair of setæ. I find, however, that in these three segments, viz. 17, 18, and 19, the ventral pair of setæ are altogether absent, although they are present in the neighbouring segments. The dorsal pair of setæ are as well developed in segments 17, 18, and 19 as in any others.

It is very common to find some modification of the setæ in the segments which bear the male generative pores, such as, for example, the bundles of elongated setæ in Acanthodrilus, but I am not acquainted with any other instance (except Eudrilus) in which the setæ entirely disappear on these segments (figs. 16, 17).

The anterior pair of glands (figs. 7, 16, *pr.*), those which occupy segment 17, and which are distinguished by their greater size and greater opacity, are the real atria; that is to say, it is these glands alone which are connected with the vasa deferentia. These glands have much the same structure as in other Earthworms; the very narrow lumen is surrounded by a layer of columnar cells; outside these is a mass of glandular cells, the exact relations of which the condition of the material does not enable me to state positively. Apparently these cells resemble very closely the corresponding cells in the prostate of Eudrilus. Outside is a delicate sheath containing blood-vessels which send off branches among the gland-cells. The atrium communicates with the exterior by a slender but thick-walled muscular duct; this duct is at first much contorted, but when it enters the body wall is perfectly straight; its course through the latter is oblique, the external orifice being placed nearer to the ventral median line than the point where the tube enters the body wall.

The tubular glands of segments 18 and 19 (figs. 7, 17, *pr.'*) are straight, and not contorted like the glands of segment 17, and their diameter is considerably less; their minute structure, however, seems to be identical, except that the glandular layer is naturally less developed.

Ovaries.—These organs (fig. 15, *o.*) occupy the usual position in segment 13; they are large and conspicuous.

Oviducts.—The oviducts (fig. 15, *od.*) open by a wide, funnel-shaped orifice into the interior of segment 13; their duct perforates the mesentery, dividing this from the succeeding segment. Each opens separately on to the exterior; the external orifices are very closely approximated, and lie within the ventralmost setæ at the same level as the apertures of the atria.

Spermathecæ.—There is only a single pair of these organs present, which are situated in the eighth segment; the external aperture, as already stated, corresponds in position to the ventral pair of setæ. The spermatheca is divided into two parts (fig. 8), a large sac lying posteriorly and opening on to the exterior in common with a mulberry-like structure which represents the diverticulum; as in so many other species of Earthworms, the diverticulum lies anterior to the pouch. The minute structure of these two sections of the spermatheca differs; the pouch itself is lined (fig. 19) with a tall columnar epithelium, which appears to resemble in every particular the lining epithelium of the spermatheca of Lumbricus. Outside this is a comparatively thin layer of muscular tissue permeated by abundant blood-capillaries; the muscular sheath gets much thicker where the pouch narrows to its external opening, and here the character of the lining epithelium alters slightly and becomes indistinguishable from the epidermis of the body surface. The structure of the numerous diverticula differs somewhat; the presence of numerous small diverticula gives to the region of the spermatheca its mulberry-like aspect. They are all, however, enclosed within a common muscular sheath (fig. 20), which is proportionately thicker than in the case of the spermatheca itself, and abundantly vascular. The diverticula are closely packed with bundles of spermatozoa, and the lining epithelium differs from that of the spermatheca itself; the epithelial cells are low and cubical. I have called attention elsewhere (7) to the fact that the diverticula of the spermathecæ in Lumbricidæ are of different minute structure to the spermathecæ, and are usually occupied by the bundles of spermatozoa which are absent from the spermathecæ themselves.

Nephridia.—The excretory system of this worm, as of so many others, differs in different regions of the body. Professor Spencer has called attention, in a paper (28) to which I shall have again to refer, to the fact that the nephridia of Megascolides are different in the anterior and in the posterior regions and of the body; this is also the case with Perichæta (p. 262) and Urochæta (p. 246); and the same condition occurs in many genera (e.g. Microchæta and Thamnodrilus) in which the nephridia consist of paired tubes, each with a single cœlomic funnel and external pore.

With regard to Megascolides, Spencer points out that the nephridia of the anterior segments present more primitive characters than those of the posterior segments, where they first begin to be modified. This statement appears to hold good (as I have already pointed out) in Acanthodrilus, and the facts which I shall bring forward in the present paper show that in Perichæta the nephridial system of the posterior segments is more modified than that of the anterior segments. In Urochæta it is only in the anterior segments that a single nephridium has more than a single ciliated funnel. With regard to such genera as Microchæta and Thamnodrilus, it is difficult to say that the anterior nephridia are in any way more primitive than those of the posterior segments.

In Dichogaster the same generalisation with respect to the nephridia appears to hold good. I am unable, however, to give so complete an account of the nephridia as I could have wished. The first five segments are occupied by a large nephridium, which evidently corresponds to the large anterior nephridium of Acanthodrilus multiporus and A. annectens. I could not find the funnels of this organ (if they are really present), nor could I find any very decided evidence of its being a branched gland. I am rather inclined, however, to believe, from the analogy of Urochæta, that it is branched. This nephridium terminates in a comparatively wide, thick-walled tube, which becomes wider and thinner walled as it approaches the external orifice, which is within the buccal cavity, as in the two species of Acanthodrilus mentioned above. In the segments of the body which follow (I am uncertain how many), the nephridial system is much like that of Acanthodrilus multiporus; that is, it consists of tufts of tubules which open by numerous apertures on the surface of the body. These apertures have no regular arrangement that I could observe; frequently they are situated near to the setæ, but as frequently they open near to the anterior or posterior boundaries of the segment. The apertures are extremely obvious, both in transverse and longitudinal sections, on account of their large size. I have not been able to observe any funnels connected with these nephridia.

In the posterior region of the body the nephridia are different, and, as already mentioned, are in certain respects more modified than those of the anterior segments.

On a dissection of this region of the worm the nephridia appeared to be separable into a number (about six) of pairs of distinct nephridia. In transverse sections the nephridial system was seen to consist of scattered tufts of tubules and of a large pair of nephridia; the arrangement being, in fact, much like that of Megascolides. The calibre of the large nephridia was many times greater than that of the small tufts, or about equal to that of the nephridia of such types as Lumbricus. Each of these large nephridia is furnished with a large ciliated funnel, which lies in the segment in front. I have been quite unable to detect the external apertures of the nephridia of these posterior segments.

The tufts of smaller tubules were not in all cases (if in any) detached from the large nephridia; their apparent distinctness, when seen in a dissection of the worm, is due to the fact that they are for the most part embedded in the centre of a mass of peritoneal cells. These peritoneal cells, which form aggregations round certain parts of the nephridia, are exactly like those which surround the nephridia of Pontodrilus, as well as of Phreoryctes. Perrier was the first who drew attention (**23**) to the resemblances in this particular between the nephridia of Pontodrilus and those of the "Limicolæ;" and Dichogaster is another instance of an Earthworm which so far approximates in the characters of its nephridia to the "Limicolæ."

III. FURTHER REMARKS ON THE NEPHRIDIA OF EARTHWORMS.

The Nephridia of Perichæta aspergillum.—With regard to the nephridia of Perichæta aspergillum, I am able to make some additions to my former papers upon this genus (**1**). The most important point which I was then able to prove is that the nephridiopores, instead of being present to the number of only one pair in each segment, are extremely numerous. I stated (**1**, p. 401) that there were often four or five nephridiopores lying between two setæ, making, therefore, a total of from one to two hundred in each segment. I have figured and described these nephridiopores as forming a continuous row round the middle of each segment. After discovering that in Dichogaster the nephridiopores are not limited to the spaces between the setæ of a segment (v. suprà, p. 259), I carefully re-examined Perichæta aspergillum with reference to this point; the result of this re-examination is to show that P. aspergillum resembles Dichogaster. The nephridiopores are scattered irregularly over every part of the body, and are not by any means confined to the area lying between the setæ of a given segment.

Ciliated Funnels.—Another fact of some little importance which I am able to add to my former paper upon Perichæta, is the description of ciliated funnels. In the posterior region of the body the funnels were extremely obvious although small; the small size of the ciliated funnel corresponds to the small calibre of the excretory tubules. These structures were obvious, for the reason that, as a general rule but by no means always, they are borne at the extremity of a very straight tubule (fig. 10). The structure of the funnels is illustrated in fig. 10. There is nothing specially remarkable about them except their small size. The presence of ciliated funnels has been already described in the genus Perichæta by Rosa (26), who found in P. armata a pair of ciliated funnels in every segment. Dr. Benham informs me that he has noticed in a species of Perichæta from the Philippines numerous funnels in each segment, corresponding to the numerous nephridia, which he has already briefly referred to (9, No. 1, p. 256) as existing in that species (which has apparently not yet been identified).

In P. aspergillum I have satisfied myself that there are a number of funnels in each segment; this, however, only applies to the segments behind the clitellum. In the anterior segments, the nephridia of which alone were described in my former paper, I am still unable, after a renewed search, to discover any evidence of the presence of ciliated funnels.

It has been stated that the ciliated funnels are of small size, but they are not all of the same size; some (fig. 10 *a*) are distinctly larger than others (fig. 10 *b*). I shall have occasion to point out directly that the nephridial tubules of these posterior segments are partly of greater calibre than those of the anterior segments; it is possible in the posterior segments to distinguish these wider tubules from the minute tubules which resemble those of the anterior segments. This accounts for the difference in size between the funnels. The larger funnels are connected with the larger tubules. It occasionally happens that the larger funnels are borne upon tubules, which immediately perforate the septum and join the nephridial tufts of the segment behind.

Comparison of the Nephridia of the Anterior with those of the Posterior Segments.

In my paper already quoted upon the nephridia of Perichæta aspergillum I have described the perforation of the intersegmental septa by tubules which connect the nephridial systems of adjacent segments. In some of the anterior segments of this Perichæta, particularly those which contain the spermathecæ, the nephridial system consists of an enormous mass of tubules which almost completely fills the available part of the cœlom. So closely are the excretory tubules packed that I have found it impossible to distinguish a series of separate nephridia corresponding to the numerous external pores. This fact, together with the perforation of the septum by tubules, led me to the impression that there must be in this region of the body a continuous nephridial network independent of the segments.

It occurred to me while making these observations, and it has occurred to me lately after discovering the ciliated funnels of P. aspergillum, that the supposed connection between the nephridial system of two adjacent segments might be really nothing more than the normal perforation of the septa by tubules, terminating on the anterior side of the septum in ciliated funnels.

This supposition, however, appears to be negatived by the following considerations: In the first place I succeeded in many cases in tracing a given tubule through the septum until it became lost in the excretory mass of the segment in front. Secondly, in the posterior region of the body the ciliated funnels are usually not borne upon the anterior face of the mesenteries in the way that is so general among Earthworms, though this sometimes happens. In most cases the long straight tube bearing the funnels rises up from a tuft of tubules, and does not perforate the septum, but ends in the same segment. Thirdly, it occasionally happens, both in the anterior and in the posterior region of the body, that a mesentery was perforated at one spot by a number of tubules running close together in irregular windings. Such masses of nephridial tubules did not pass between the individual muscular fibres of the septum, but the continuity of the tissues of the septum was broken at the point where they traversed it. A conspicuous gap was thus formed, which was entirely occupied by the nephridial tubules and peritoneal cells coating them. In these cases it appeared to me that the bundle of tubules passing through the septum was not formed by the coils of a single tube, but that it really represents a number of separate tubes running side by side. On the assumption that the perforation of the intersegmental septa by nephridial tubes is not evidence of an intercommunication of the nephridia of successive segments, one would have expected to find a number of funnels dependent from the septum at this point. I could not, however, detect these structures, and in the posterior region of the body, as already stated, the funnels are rarely attached to the septa.

The probability of my statements being correct is also largely increased by the discovery of Professor Spencer (28), that in Megascolides australis there is a continuous network of nephridial tubules uninterrupted by the septa.

The observation of the nephridial tubules within the thickness of the septum is not always easy. In some cases, however, they are accompanied by a tolerably thick coating of peritoneal cells, when they can be readily detected. I have found that in the anterior region of the body it is easier to trace the tubules from segment to segment in transverse sections. In the case of the larger tubules of the posterior segments the branches connecting the tufts of adjacent segments are not difficult to make out.

In the posterior region of the body the nephridia are not so well developed as they are anteriorly. The nephridial tubules are, however, much like those of the anterior segments (unless there are really no funnels in the anterior segments), but they are closely attached to the body wall, and particularly to the septa. They do not occupy a large portion of the body-cavity. I have ascertained by sections, as well as by an examination of stripped-off pieces of cuticle, that the nephridiopores have the same irregular distribution that they have in the anterior segments. Furthermore, there is, as has been mentioned, an intercommunication between the nephridial tufts of successive segments. I have observed frequently a connection, by tubules traversing the septum, between two nephridia adherent to opposite sides of the same septum. At the same time it appears to be certain that in the nephridia of these segments there is no longer an intimate connection between all the nephridial tubules of the same segment. An examination of a series of sections shows that there are tufts of tubules which are quite isolated from neighbouring tufts. On the other hand, there is—as has just been said—frequently no break between nephridial tufts of adjacent segments. These facts appear to me to be of some importance with regard to the views which I have elsewhere (1) advanced as to the origin of the Oligochæt excretory system. We have here, as it appears to me, a commencing separation of the continuous excretory network into isolated nephridia. This breaking up has at first no relation to the segmentation of the body. The nephridial tufts have no regular arrangement within the segment, and their apertures are dotted about irregularly over its surface, and the separation into separate nephridia does not follow the lines of the intersegmental septa. The excretory system, in fact, appears to retain, longer than many other organs of the body, traces of the primitive unsegmental condition.

For the most part the nephridia of the posterior segments have the same appearance as those of the anterior segments, that is to say, they consist of tufts of tubules having an excessively fine bore. There are, however, tubules of greater calibre which appear to be wanting in the anterior segments. In this particular there is a resemblance between P. aspergillum and Megascolides (Spencer). In that genus the posterior segments of the body contain nephridial tubules which are much larger than others in the same segments, and than all in the anterior segments of the body. There is also the further resemblance that the tufts of larger tubules are connected with funnels which project into the segment in front. In Perichæta, however, the smaller nephridial tufts also possess funnels, which they apparently do not in Megascolides. Until the publication of Professor Spencer's illustrated account of Megascolides it is impossible to say how far this resemblance in the specialisation of the nephridia goes. The difference in size is not very marked in P. aspergillum, not nearly so much so as in P. armata.

In my paper upon Perichæta aspergillum I have not figured the cuticular pores of the nephridia, and so I have thought it worth while to introduce into the present paper illustrations of their structures. Fig. 23 of Plate XXIV represents a portion of the cuticle of P. aspergillum, showing the cuticular ingrowths which surround the proximal region of the seta (*a*), and the very delicate cuticular tube (*b*) which lines the extremity of the duct of the nephridium. When these structures are viewed from above the aperture, whether of the seta or of the nephridium, they appear to be surrounded by a thickened layer of the cuticular membrane. This is, I believe, only an optical effect due to the inturned edges of the cuticle. It seems, however, to define very plainly the orifice. The very great size of the seta orifice, as compared with that of the nephridiopore, will be evident from an examination of the figure cited. The cuticular pore of the nephridium is further remarkable for the fact that its edges are usually much crinkled, which is probably due to the contraction of the epidermic cells by the preservative reagent. The cuticular pores which lead into the seta sacs never show these crinkled edges, probably for the reason that they remain distended by the seta.

Having ascertained that these cuticular pores belong to the nephridial system, I have examined the cuticle of another species of Perichæta of which I possess examples not sufficiently well preserved to show the modifications of the epidermal cells round the nephridiopore. I find that they are present in Perichæta Houlleti, and I consider myself therefore at liberty to infer that in this species (and, indeed, probably in all Perichæta in which the nephridia have a "tufted" character) the structure of the nephridial system is much the same as that of P. aspergillum.

In Acanthodrilus and Dichogaster the external orifices of the nephridial system are larger than those of Perichæta and (judging from Spencer's description) of Megascolides;

their greater size renders them very plainly visible in transverse and longitudinal sections of the body wall and upon fragments of the cuticle. The cells surrounding the orifice are tall, thin cells, not bulged like those of Perichæta and Megascolides.

The Nephridia of Perichæta armata (F. E. B.).—I owe the material, upon the study of which the present description is based, to the kindness of Mr. W. L. Sclater, of the Indian Museum, Calcutta.

The species was first described by myself, and has been recently in some respects more fully characterised by Rosa (**26**).

There is, however, one point in which Rosa's description differs from my own. I stated that the nephridia, at least in the anterior region of the body, consisted of numerous tufts of tubules, resembling in this particular the nephridia of the greater number of species of Perichæta. The characters of the nephridia in the specimens examined by me was such that I should have presumed—in the light of my own subsequent investigations—that the number of nephridiopores in each segment would be greater than two.

On the contrary, Rosa's description of those organs shows that he considers them to be like those of Lumbricus, i. e. a single pair to each segment. He describes, and I can confirm the accuracy of his description, the presence in each segment of a pair of coiled nephridia, each of which opens into the segment in front by a ciliated funnel. Rosa was unable to find the external pores. So far I can fully bear out the statements made by Rosa; but this description of the nephridial system of P. armata is not exhaustive. It consists also of numerous tufts of minute tubules which are scattered about irregularly in the segments. These tubules are not obvious on a dissection of the worm, but they are quite easily seen in transverse sections.

The nephridial system of Perichæta armata differs in important particulars from the nephridial system of any species of Perichæta; it differs from that of P. aspergillum (see p. 265) and an undescribed species briefly referred to by

Benham (9, No. 1) in the presence in each segment of a pair of large nephridia, opening by a funnel into the segment in front, in addition to the tufts of minute tubules present in these types. In one or two species from Australia, described by Mr. Fletcher (16), only the large pair of nephridia are present. The minute tufts of tubules are unrepresented.

There is, however, a close resemblance between the nephridia of P. armata and those of Megascolides australis, which have been briefly described in a note published in 'Nature' of June 28th, 1888, by Professor Baldwin Spencer. I have not yet had the opportunity of seeing Professor Spencer's detailed memoir upon this most interesting genus of Earthworms, but the note referred to is an abstract of the more important results of his investigation of the nephridial system.

It appears that in the anterior segments of Megascolides there are abundant scattered tufts of minute nephridial tubules, which are connected by a network lying within the peritoneum and extending from segment to segment. In the posterior segments of the body there are in addition a pair of coiled nephridial tubes of a very much greater calibre than the minute tubules. Each of these opens by a funnel into the segment in front, and they are connected by a continuous longitudinal duct which runs from segment to segment. These larger nephridia, as well as the longitudinal duct, are also in connection with the system of minute tubules; the latter have no ciliated funnels but open externally by numerous pores.

In P. armata I have not actually traced the nephridial tubules through the body wall to their point of opening on to the exterior. I have, however, found upon the cuticle the nephridiopores, which were abundant in each segment, and agreed in all particulars with those of P. aspergillum (see p. 265), so that I cannot admit any doubt as to the resemblance in this particular between the nephridia of P. armata and those of P. aspergillum. I have also been unable to detect any ciliated funnels except those belonging to the large pair of nephridia. In all these points, therefore, there is an agreement with Megascolides. But the nephridial tufts of P. armata appear to be at any rate largely isolated from each other and from the pair of large nephridia; and I have not found a longitudinal duct passing from the large nephridia of successive segments and connecting them. Neither can I discover evidence of any nephridial network uniting the tufts of minute tubules of successive segments. In all these points the nephridia of P. armata are different from those of Megascolides. I shall refer again to the nephridia of P. armata and to Professor Spencer's description of Megascolides (see below.

Comparison of the Nephridia of Perichæta, Megascolides, Acanthodrilus multiporus, Deinodrilus, Dichogaster.

Before attempting to draw any conclusions as to the path of development of the excretory system in Earthworms, it will be convenient to briefly review the facts already known concerning the nephridia of those genera in which there is a greater or less development of a network with numerous external pores in each segment.

It appears to be possible to separate those genera into two groups: the first group contains Perichæta and Megascolides; the second, the remaining genera enumerated above. I am at present uncertain as to the relations of Typhæus, which has not yet been properly investigated.

The principal character which distinguishes the nephridia of these two groups is the size of the tubules.

In Perichæta, and apparently also in Megascolides, the greater part of the nephridial system (the whole of it in the anterior segments of the body) is made of tubules having an excessively fine lumen; the entire diameter of the tubules is not inconsiderable, but the perforation of the cells which form the duct is much less than the thickness of its walls. Besides the network of fine tubules, both these genera possess coils of tubules of a much greater diameter which are more or less closely connected with the network of fine tubules; that is to say, they form a more or less independent nephridium opening internally in Megascolides and Perichæta armata by a single funnel.

In Deinodrilus, Acanthodrilus, and Dichogaster, the general nephridial network is made up of tubules, the lumen of which is greater than in Perichæta; the diameter of the cells is not greater, but the lumen occupies a greater proportion of the cell. These tubules resemble in fact very closely the finer portion of the nephridium of Lumbricus. In Deinodrilus (at any rate in those segments of the body which I have investigated—some of the more posterior ones) the nephridial network appears to be entirely made up of tubules of this kind. In the other two genera, however, part of the nephridial network is composed of tubules of a much greater calibre, equal in size to the larger tubules of P. armata, or of such Earthworms (e.g. Allurus, Pontodrilus, Eudrilus, Acanthodrilus novæ-zealandiæ) as possess but a single pair of nephridia in each segment of the body. In Acanthodrilus multiporus the larger tubules are not independent of the smaller tubules, and the network opens into the cœlom by numerous funnels, as in Perichæta aspergillum. In Dichogaster, in the anterior segments, this specialisation of the network is not seen; in the posterior segments, on the other hand, there is not much beyond the coil of large nephridial tubules, which have to a great extent the characters of a single nephridium, such as that of Lumbricus, &c., and open into the cœlom by a single funnel borne at the end of a duct which traverses the intersegmental septum.

We have therefore a parallel series in the nephridia of these two groups which may be expressed in the following Table:

A. Nephridia forming a network, consisting of excessively fine canals, continuous from segment to segment.	B. Nephridia forming a network consisting of wider canals, discontinuous at the septa.
(1) ?	(1) No further specialisation. Deinodrilus.[1]
(2) Nephridial network of posterior segments, partly composed of tubules of greater calibre. Numerous cœlomic funnels. Perichæta aspergillum.	(2) Nephridial network, partly composed of tubules of greater calibre. Numerous cœlomic funnels. Acanthodrilus multiporus.
(3) Larger nephridial tubules increased in size and forming a nephridium nearly independent of the finer tubes, and opening by a single cœlomic funnel. P. armata, Megascolides.	(3) Nephridial network of posterior segments, chiefly composed of larger tubules, opening by a single cœlomic funnel. Dichogaster.

The nephridia of Acanthodrilus multiporus, of Dichogaster, and of Deinodrilus, are formed of tubules which, as said, are on the whole of greater calibre than those of Perichæta. The measurements may be approximately determined by a comparison of figs. 11–14. At the same time the nephridia of these types present other differences from Perichæta. The network is much reduced in extent and in two ways. First, only a limited area of each segment is occupied by the nephridia. They are by no means so abundantly developed as in Perichæta, not nearly so abundantly developed as in the anterior segments of Perichæta aspergillum. Secondly, the intercommunication from segment to segment has disappeared in Acanthodrilus and Dichogaster, and has almost disappeared in Deinodrilus. In the last-mentioned genus the nephridia are attached to the anterior wall of their segment, and are, for the most part, entirely restricted to this situation. In one or two instances, however, a small tuft of tubules was attached to the posterior wall of a segment; and in these cases (which are not at all

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[1] The apparent absence of cœlomic funnels in this genus may perhaps be a secondary modification.

numerous) the tuft of tubules attached to the posterior wall was in communication through the septum with the nephridium of the segment behind. This seems to me to indicate that the nephridial system of Deinodrilus is in a more archaic condition than that of either Acanthodrilus or Dichogaster. In Deinodrilus the primitive disposition of the excretory system of Perichæta has been so far retained that there is still an intersegmental communication here and there. The metameric arrangement of the nephridial system is not so complete as in Acanthodrilus and Dichogaster, though, for the matter of that, neither of these forms have an excretory system perfectly metameric in its disposition.

Another point of difference between the excretory system of Perichæta on the one hand, and that of Acanthodrilus, Deinodrilus, and Dichogaster, is in the form of the external orifices.

Professor Spencer (28) described the external orifices of the nephridia of Megascolides in the following words: "The external opening itself is formed of cells of the epidermis, so modified as to present very much the external appearance of a taste-bulb; that is, they form a sphere with the cells thicker in their middle parts, and the two ends attached to the poles of the sphere, the duct passing right up through the centre."

This description applies very closely to the modified epidermic cells which surround the nephridiopores of Perichæta. When I first observed these cells in Perichæta I thought for a moment that they really belonged to sense organs. The cells are so much swollen in their middle parts that the duct which forms up between them is of an excessively fine bore; for this reason it is not always easy to detect upon fragments of the cuticle the actual orifice.

The Evolution of the Excretory Organs in Earthworms.

I shall now proceed to deduce, from the facts described in the present paper and in Professor Spencer's account of Megascolides, what I believe to have been the course of development of the nephridial system of Earthworms.

In my paper upon Perichæta (1) I pointed out that the facts therein described were in favour of the assumption that the presence of a single pair of nephridia per segment (e. g. in Lumbricus) was the last stage of a reduction of an excretory system like that of Perichæta; and that the excretory system of Perichæta was distinctly comparable to that of the Platyhelminths. With regard to the first point, Professor Spencer's observations are, as he has pointed out, decidedly confirmatory of that view. Indeed, the nephridial system of Megascolides appears to me to be hardly intelligible on the hypothesis that Lumbricus represents the primitive condition.

Dr. Hugo Eisig's magnificent monograph of the Capitellidæ (15), which has just been published, contains a very detailed discussion of the nephridial question. It must be confessed that the structure of the nephridia in the Capitellidæ might be equally well explained on the hypothesis that the ancestral condition of the Annelid nephridial system is represented by a pair of distinct nephridia in each segment. And this is the position which Dr. Eisig takes up. The branching, whether of the distal or proximal end of the nephridium, and the connection between nephridia of the same segment, as well as the multiplication of the latter, he regards as secondary. It appears to me that this position may be safely yielded without affecting the strength of the converse view which is maintained in the present paper. I believe it to be unnecessary to assume that the Oligochæta and the Polychæta have been derived from the same Annelid stock: I hold that the ancestral form from which they diverged was intermediate between the Platyhelminths and Annelids. There is no difficulty in drawing a sharp line of division between the Oligochæta and the Polychæta. The peculiarities of the reproductive system will be the basis of this distinction. The investigations of Korschelt, Meyer, and Weldon upon Dinophilus have gone a long way towards demonstrating that this worm stands at the base of the Polychæt series. Now, the nephridia of Dinophilus are in their minute structure comparable to those of the Platyhelminths; in most species they form a single pair of branched organs terminating in numerous "flame-cells." In D. gyrociliatus, according to Meyer, each single nephridium is broken up into a series metamerically arranged, and each opening by a separate external pore. This I believe to be the way in which the Polychæt nephridia have arisen.

There is no known form which seems to me to represent an intermediate stage between the Oligochæta and the Platyhelminths. On the whole, it must be admitted that certain of the aquatic Oligochæta, such as the Naidomorpha, stand at the base of the Oligochæt series. The fact that the nephridia of these Annelids are paired is a difficulty in regarding Perichæta as representing in the structure of its nephridia an ancestral form. It must be remembered, however, that our knowledge of the aquatic Oligochæta, though no doubt fairly advanced as regards indigenous forms, is very small as regards exotic genera. Also there are traces (in Anachæta, Vejdovsky (29) (Pl. VII, fig. 14) of what I believe to be the primitive condition. It may be that the (presumed) reduction of the nephridia in these aquatic forms has some relation to their small size, and, in consequence, to the reduced size of the cœlomic cavities.

It will be of no advantage to endeavour to combat Dr. Eisig's arguments against regarding the nephridia of Acanthodrilus multiporus as representing an archaic condition, principally for the reason that at the time when he wrote he was able to say that only one or two genera exhibited the dysmetameric condition, the vast majority having a metameric condition of the nephridia.

We are now, however, acquainted with the following genera in which the nephridia are often or always dysmetameric:—Perichæta, Acanthodrilus, Typhæus, Deinodrilus, Dichogaster, Megascolex (?), Megascolides, Notoscolex, while traces of the same are to be seen in Urochæta. The argument of the rarity of the occurrence of the dysmetameric nephridia cannot any longer have any weight, and his detailed criticisms, though powerful at the time, are now, through the progress of discovery, of less weight. His other arguments depend chiefly upon the fact that this condition is only found among the Polychæta in the Capitellidæ. Regarding, as he does, the Capitellidæ as nearly akin to the Oligochæta, and in fact forming the intermediate link between them and the Polychæta, this argument is a powerful one. I find myself, however, unable to accept this position. The peculiarities of the reproductive system in the Oligochæta, coupled with the entire absence of parapodia and external gills, distinguish them from the Polychæta. Dr. Eisig compares the peculiar modification of the integument which surrounds the genital pores with the clitellum of the Oligochæta. I would myself rather compare it with the modified integument which surrounds the aperture of the vas deferens in Allurus and Allolobophora; but I do not think that the possibility of this comparison is necessarily a mark of near affinity. The comparison between the nephridia of the Capitellidæ and those of Acanthodrilus does not really show a very close resemblance; the structure of these organs is so peculiar, as Eisig has shown, that it renders a detailed comparison difficult, as does also the fact that they are often preceded by a provisional set. Indeed, I cannot help agreeing with Dr. Eisig that their modifications in the Capitellidæ are secondary, though I would maintain that this is not the case with Urochæta, Acanthodrilus, &c.

The nearest approach to the primitive condition of the excretory system in the Oligochæta is, in my opinion, seen in Perichæta aspergillum; in the anterior segments the resemblance to the Platyhelminth excretory system is closest. There is here a continuous network of tubules, with numerous external pores. The network is not interrupted by the septa, and the external pores are not in any way related to the segmentation of the body. If funnels are really absent, as appears to be the case, then the termination of the tubules in single cells will be an additional point of resemblance to the Platyhelminths; if, on the contrary, funnels are really present, they must be small and inconspicuous and not much advanced beyond the single flame-cell.[1]

In the posterior segments part of the nephridial network consists of tubules of a greater calibre, and these, as well as the smaller tubules (which are exactly similar to those of the anterior segments), are provided with funnels. The external apertures are still extremely numerous, and irregularly distributed over the surface of the body. The network of tubules is beginning to break up into more or less isolated tufts; but the separation of the continuous network into isolated nephridia has no discernible relation to the segmentation; the tufts of tubules have no regular arrangement within the segment, and the septa do not as yet form barriers between the excretory tubes of different segments.

In the posterior segments, therefore, the primitive characters of the nephridial system are just beginning to disappear. If the posterior segments resembled the anterior segments the nephridial system of P. aspergillum would exhibit the presumed ancestral condition.

From this point the modification of the excretory system has, as I think, proceeded along two slightly divergent paths; the ultimate point reached, however—the reduction of the nephridial system to a pair of isolated nephridia in each segment—is the same in both cases. The facts known appear to

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[1] I have already (1) discussed the "funnel" of the Annelid nephridium and its relation to the Platyhelminth flame-cell. Since that paper was written Vejdovsky has published ('Zool. Anzeiger,' Bd. x) an account of the nephridia of certain Oligochæta. The "provisional" nephridia, which are preceded at the anterior extremity of the body by a "larval" set, terminate in a flame-cell. These nephridia entirely disappear in the first two or three segments; behind this they become converted into the permanent nephridia; the flame-cell divides and gives rise to a funnel.

me to necessitate this view of the gradual reduction of the excretory system; it is difficult to harmonise the facts with the hypothesis of one continuous line of development.

It is obvious that any theory of the development of the nephridia must allow for the reduction of the nephridial network in Perichæta aspergillum to a single pair of nephridia, such as is found in P. novæ-zealandiæ,[1] and also in the genus Perionyx, which is in all respects a very near ally of Perichæta; and this reduction must not involve the various stages represented by Deinodrilus, Acanthodrilus, and Dichogaster, though these are intermediate between P. aspergillum and P. novæ-zealandiæ.

The intermediate stage between P. aspergillum and P. novæ-zealandiæ is represented by P. armata. In this Perichæta the nephridia of the posterior segment are, as Spencer pointed out in the case of Megascolides, separable into two categories; firstly, there are the tufts of minute tubules; secondly, a pair of convoluted nephridial tubes, with a ciliated funnel borne upon the extremity of a tube which has traversed the septum, and lying in the segment anterior to that which contains the nephridium; these latter are of the same calibre as the nephridia of P. novæ-zealandiæ, and indeed of most Earthworms in which there is but a single pair of nephridia per segment. I believe that these have originated from the somewhat larger nephridial tubules of such a form as P. aspergillum; the minute nephridia form tufts which are largely, if not entirely, isolated from each other and from the large nephridia; they are comparatively inconspicuous, and seem to be in course of disappearance. Megascolides offers an analogous stage in the development of a single pair of nephridia out of the nephridial network. I quite agree with Spencer that the single pair of nephridia of certain Earthworms (e.g. Perichæta novæ-zealandiæ and Perionyx) have arisen by a gradual increase in

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[1] This is an apparently new species of Perichæta, which I hope to describe shortly; it possesses a single pair of nephridia per somite, as in Lumbricus.

calibre of a part of the nephridial network in each segment to form a pair of nephridia, and by the gradual disappearance of the rest.

The second way in which I conceive the gradual reduction of the network to a single pair of nephridia to have been brought about is as follows:

The network became arranged metamerically by the isolation of the networks of successive segments at the septa; at the same time the tubules themselves acquired a greater calibre. This stage is nearly reached in Deinodrilus, where the nephridial system forms a continuous series of tufts attached to the anterior wall of each segment; but here and there in Deinodrilus the nephridia are connected through the septa with feebly-developed tufts of tubules lying on the posterior side of the segment in front.

In Acanthodrilus multiporus this stage is exemplified; all trace of the intercommunication between the nephridial systems of successive segments through the septa is lost, and the tubules are uniformly of greater calibre than those of Perichæta; at the same time they are more decidedly related to the setæ of their segments. From this point the paired nephridia of other species of Earthworms have been derived either by a great increase in the calibre of the tubules coupled with the disappearance of part of the network and all the external orifices, except a pair to each segment (Dichogaster seems to be a stage further advanced than Acanthodrilus in the direction of those worms with a single pair of nephridia in each segment),[1] or by the breaking up of the network into separate nephridia. Brachydrilus (Benham, 10) offers an intermediate condition in this reduction; the nephridial network has been broken up so as to form two separate pairs of nephridia in each segment. One pair then disappears, and the typical condition of the Earthworm excretory system is arrived at.

I am disposed therefore to believe that the paired

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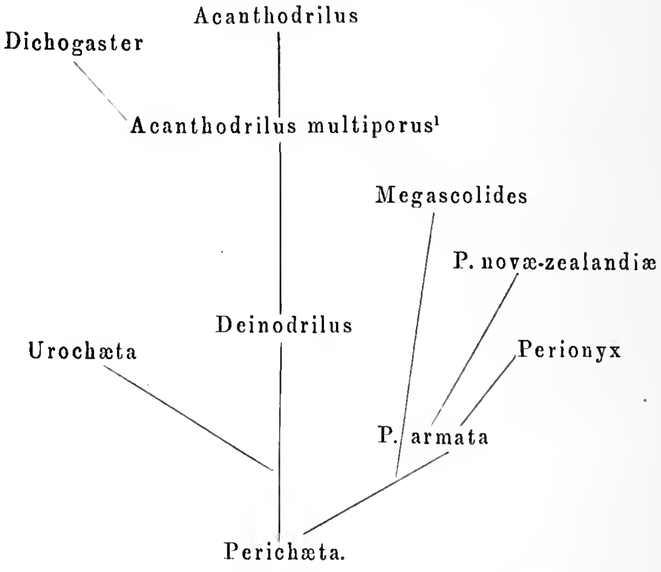
[1] I have elsewhere (8) called attention to other points in which Deinodrilus is intermediate between Perichæta and Acanthodrilus.

nephridia of certain other Earthworms (e.g. Acanthodrilus novæ-zealandiæ) have been derived through the gradual increase in calibre of the tubules forming the primitive network, which has become isolated into metamerically disposed tufts of tubules, corresponding more or less to the setæ; these separate nephridia have become ultimately reduced to a pair in each segment.

In the first case, therefore, the single pair of nephridia have been derived directly from a part of the primitive network; in the second case the primitive network has become converted into a single pair of nephridia in each segment by a more gradual series of changes.

The annexed scheme shows the relationship between certain genera of Earthworms, as indicated by their excretory system.



This scheme, as will be seen, only refers to the genera which

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[1] It is possible that this species is really a distinct generic type. It has no paired setæ like the other species of the genus. If so, A. annectens (Beddard, 8) should probably be referred to the same genus.

have been specially treated of in the present paper. I do not feel able at present to extend the diagram so as to embrace all the known genera, or even the greater number.

I would point out, however, that the above scheme, though meant only to express the probable course of the development of the excretory system, does not do violence to the relationships in other structural characters between the different genera.

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EXPLANATION OF PLATES XXIII & XXIV,

Illustrating Mr. Frank E. Beddard's paper "On Certain Points in the Structure of Urochæta, E. P., and Dichogaster, n. g., with further Remarks on the Nephridia of Earthworms."

PLATE XXIII.

Fig. 1.—Semi-diagrammatic longitudinal section through anterior extremity of Urochæta corethrura. The aperture of the mucous gland at *o* is correctly drawn as regards its position relative to the setæ, but it should be more ventral in position. *n.* Ventral nerve-cord. *f.* Funnels of mucous gland (3). *g.* Gizzard. *s.* Setæ. *c.* Supra-œsophageal ganglion. *al.* Cavity of anterior end of the alimentary tract.

Fig. 2.—Longitudinal section through genital segments of the same species. The vesiculæ seminales are not represented. *t.* Testis. *o.* Ovary. *ov.* Oviduct pore. *v. d.* Vas deferens. The segments are numbered.

Figs. 3 and 4.—Contents of genital glands of the same specimen. Both testes and ovaries have produced ova in this individual.

Fig. 5.—A funnel of the mucous gland of Urochæta.

Fig. 6.—Transverse section through body wall of Dichogaster Damonis. *e.* Epidermis. *m.* Circular muscles. *l.* Longitudinal muscles. *p.* Peritoneum.

Fig. 7.—Dichogaster. Segments in the neighbourhood of the male reproductive pores. *v. d.* Vasa deferentia. *pr.* Atria. *pr'.* Glands in 18th and 19th segments, similar in structure to the atria, but unconnected with the vasa deferentia.

Fig. 8.—Dichogaster. Ventral external view of segments in the neighbourhood of the male reproductive pores, to show pores upon the 17th, 18th, and 19th segments.

Fig. 9.—Fragment of nephridium of ditto, with glandular peritoneal cells (*a*).

Fig. 10.—Perichæta aspergillum. Nephridial funnels, *a* smaller, *b* larger. In *a* one of the two funnels, that to the right, is seen in longitudinal section.

Fig. 11.—Perichæta armata. Large nephridia of posterior segments. *a.* From a glycerine preparation, which showed very clearly the boundaries between the successive "drain-pipe" cells.

PLATE XXIV.

Fig. 12.—Perichæta aspergillum. Nephridial tube. *a*, with larger, *b*, with smaller lumen.

Fig. 13.—Deinodrilus Benhami. Nephridial tubes from posterior segment.

Fig. 14.—Acanthodrilus multiporus. Nephridial tubes. *a*, with small lumen; *b*, with wider lumen; *c*, represents the greatest size to which the nephridial tubes of this species reach.

Figs. 11—14 are all carefully drawn to scale with camera lucida.

Fig. 15.—Dichogaster. General view of genital segments dissected. The upper wall of the seminal reservoirs is removed on the left side to show the funnels and testes. *r*. Seminal reservoirs. *r'*. Seminal reservoirs of a racemose appearance. *t*. Testes. *f*. Funnel of vasa deferentia. *o*. Ovary. *od*. Oviduct.

Fig. 16.—Transverse section of body of the same worm at the line of the atria (*pr.*). *v. d.* Vasa deferentia joining the muscular portion of atria.

Fig. 17.—Corresponding section through nineteenth segment. *pr'*. Glandular body.

Fig. 18.—Spermatheca with appendix, *a*.

Fig. 19.—Transverse section through wall of spermatheca.

Fig. 20.—Transverse section through appendix of spermatheca.

Fig. 21.—Anterior region of alimentary canal, to show two gizzards, *g.*, and calciferous glands, *Ca*.

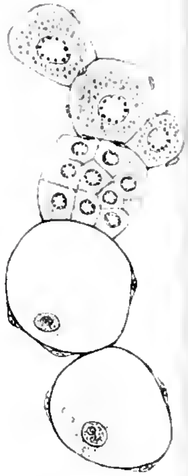
Fig. 22.—Ova of different species of Oligochæta, to illustrate their relative sizes. Drawn to scale. *a*. Of Urochæta corethrura, from cœlom. *a'*. Largest ova from ovary. *b*. Of Phreoryctes Smithii, from ovary. *c*. Of Allurus. *c*. From receptaculum ovorum. *c'*. From ovary. *d*. Of Eudrilus, from ovary. *e*. Of Acanthodrilus, from ovary.

Fig. 23.—Fragment of cuticle of Perichæta aspergillum. *a*. Orifices of setæ. *b*. Nephridiopores.

Fig. 24.—Perichæta aspergillum. Diagram to illustrate nephridia of posterior segments. *o*. Nephridiopore. *f*. Funnel.

Fig. 3.

Fig. 1.



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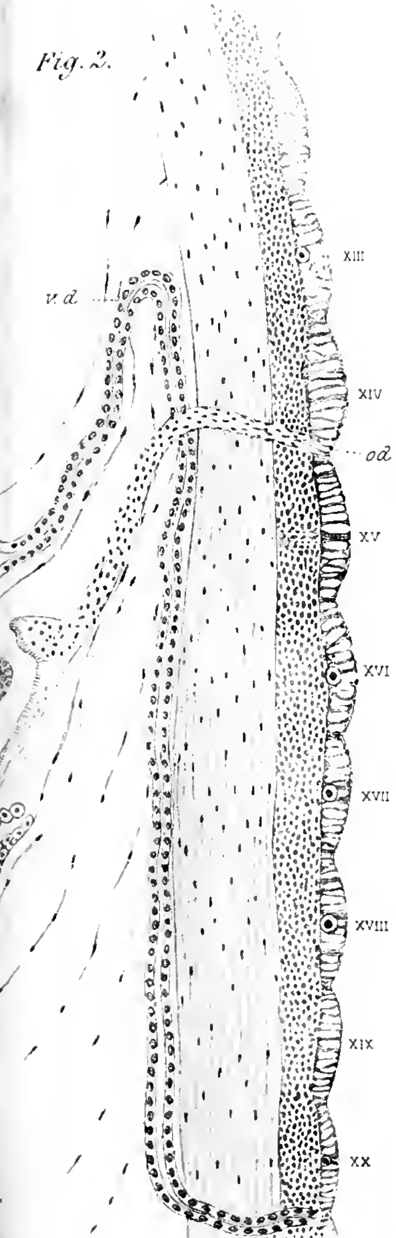

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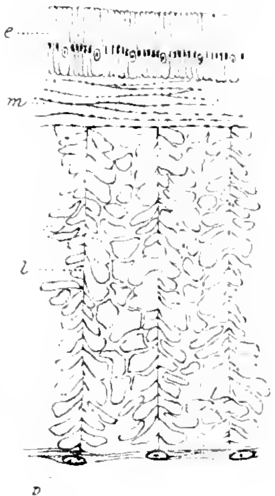

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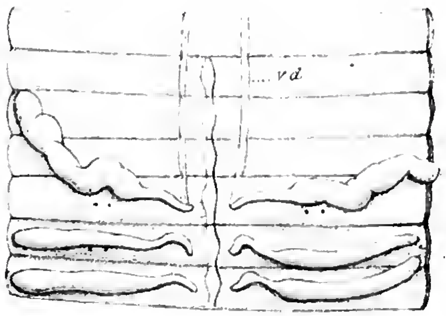

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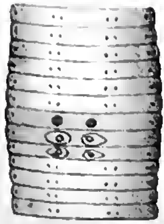
Fig. 11.



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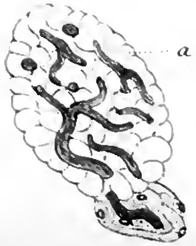


Fig. 9.

Fig. 10.

F. E. Beddard del.

F. Huth, Lith^r Edin^r

Fig. 13.

Fig. 14.

Fig. 15.

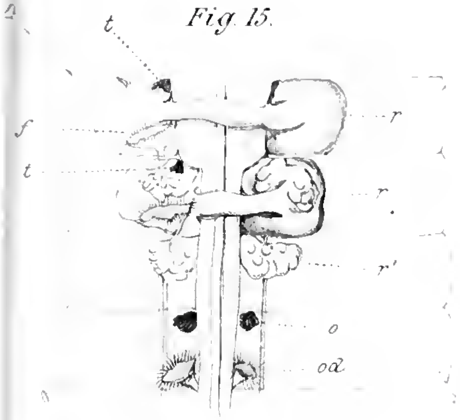


Fig. 12.

Fig. 18.

Fig. 19.

Fig. 21.

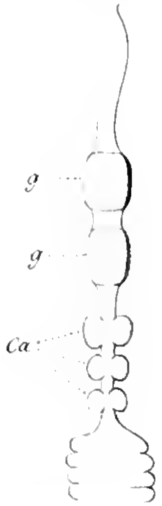


Fig. 20.

Fig. 22.

Fig. 16.

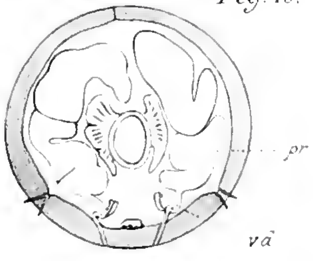


Fig. 17.

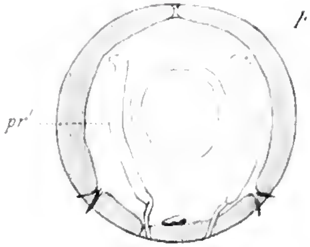


Fig. 23.

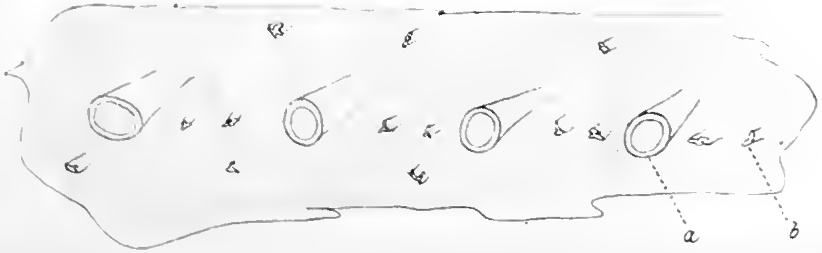
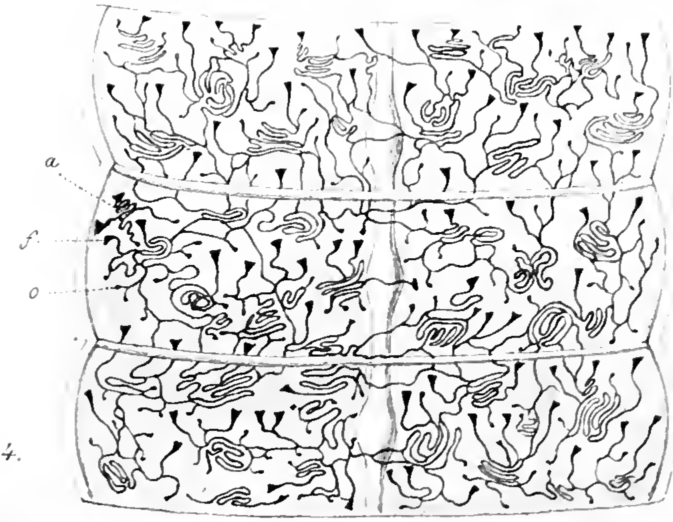


Fig. 24.



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On the Development of Peripatus Novæ-Zealandiæ.

By

Lilian Sheldon,
Bathurst Student, Newnham College, Cambridge.

With Plates XXV and XXVI.

In January last, through the kindness of Mr. Sedgwick, I received another supply of Peripatus novæ-zealandiæ. As before, they arrived in the living condition, and the eggs were removed from the uterus immediately after the animal had been killed with chloroform.

The proportion of males was considerably larger than on previous occasions, being twenty-two out of a total of forty-nine. There were nine smallish females which contained no embryos; and in the remainder, which varied in size from about three-quarters to two inches in length, the uteri were filled with embryos. The number of embryos in a single female varied considerably, the maximum being eighteen and the minimum seven.

Most of the embryos were preserved in corrosive sublimate and glacial acetic acid used hot, but the best results were obtained from some which were placed for six or seven hours in a mixture consisting of equal parts of ·5 per cent. chromic acid and 2 per cent. acetic, and afterwards washed in alcohol. In this method it is not necessary to prick the egg-shell before the embryo is removed to alcohol. After this method of preservation, which is that recommended by Hertwig for amphibian eggs, the yolk is rendered much less brittle than after any other methods which I have tried; the protoplasm and nuclei are well preserved, and also the egg-shell expands and lies at some distance from the periphery of the ovum, and so can easily be removed. The eggs were all stained with picro-carmine, and passed through the various strengths of alcohol in which a small quantity of picric acid was dissolved.

The embryos, with the exception of a few quite old ones, were all of stages between those shown in figs. 10 and 15 in my last paper (4), that is, they came in age between those received in December and April respectively.

My material is again very incomplete, and the new stages which I shall describe, though they throw some light on the early development, are very few, and do not unfortunately by any means fill up the gaps which were left in the account of the development given in my last paper (4); but it seemed advisable to publish my results, in the hope that they might prove useful if anyone should have the opportunity of working on the development of this interesting species with a better supply of material than I have been able to obtain.

The ovum, which represented the latest segmentation stage, described and figured (fig. 10) in my last paper (4), was one which was taken out of the uterus in December. In it the nuclei were present round slightly more than half the ovum, lying in small masses of branched protoplasm. The central one of these nuclei lay on the surface and showed signs of karyokinetic figures. There were also two or three protoplasmic masses in the central yolk. I have now (in the January lot) several stages later than this, which show that the nuclei in the centre of the surface of the ovum beneath which they lie multiply with considerable speed and very much more quickly than those over the rest of the ovum, a condition which is shown in fig. 4, until by their repeated increase the egg acquires the form shown in fig. 11 (4), which represented a transverse section through an April ovum. In the ovum there figured there is a specially-marked area of reticulate protoplasm, containing a large number of nuclei extending through about one third of the length of the ovum, and having in transverse section an irregular triangular shape, the base of the triangle resting on the surface; nuclei are also present throughout the yolk, more especially near the periphery.

As was said in (4) the protoplasmic area next becomes more compact and flattened out against the side of the ovum, so as to form a kind of plate of fairly dense protoplasm which is closely packed with nuclei, and which lies on the surface at one side of the ovum through about the middle third of its length: this is shown in transverse section in fig. 13 (4), which is from one of the ova taken out in April.

A good many of the January eggs were of stages which came after this last. The protoplasmic area begins to grow round the surface of the egg until, as is shown in fig. 1, it covers nearly half the periphery. The nuclei in the central region of this protoplasmic area are two or three deep, but towards its edges the protoplasm thins gradually and the nuclei form only one layer. The ovum is closely packed with yolk, among which a few nuclei are irregularly scattered. The process of epibolic growth of the protoplasmic area continues, so that, as is shown in fig. 2, still more of the periphery of the egg becomes covered with the thin layer of protoplasm which may be called the blastoderm, until when the growth of the latter ceases only a very small portion is left uncovered.

The blastoderm now consists of a thin layer of protoplasm, in which a single layer of flat nuclei is present, extending round the whole periphery of the egg with the exception of a small space lying in the centre of one side of the egg in which the yolk is left uncovered. This uncovered space corresponds with the position of the future blastopore, and is, I believe, situated on the ventral side of the embryo, thus agreeing with other Arthropods, except the Scorpions, in which the blastopore is situated dorsally.

A change now takes place in the blastoderm behind and at the sides of the uncovered area. In the middle line behind this area a proliferation of the nuclei takes place extending some distance backwards, so that a keel-shaped mass of nuclei embedded in a loose reticulum of protoplasm is present in about the posterior half of the ovum; this condition is shown in transverse section in fig. 3. The nuclei at the sides of the area also proliferate, as is shown in fig. 3 *a*, which represents a transverse section through this region from the same ovum as fig. 3, but is drawn under a higher power.

The proliferating mass of nuclei increases in size and occupies a larger portion of the surface of the ovum, and both nuclei and protoplasm are closer and more compact; a transverse section through the posterior half of such an ovum is shown in fig. 8. At the same time the protoplasm at the sides of the uncovered area become slightly inflected; this is shown in fig. 9, which is a transverse section through this region from the same ovum as fig. 8, but drawn under a higher power. The uncovered area thus forms a passage lined by the cells of the blastoderm, which have become inflected, and leading into the yolk; it may be spoken of as the blastopore, as is the case in P. capensis it is traversed by strands of protoplasm.

These two structures, i. e. the blastopore and the area of proliferating cells lying posterior to it, soon acquire very close resemblance to the blastopore and primitive streak of P. capensis, with which they are probably homologous. The blastopore increases in length and the protoplasm at its sides shows a true invaginate character, and a groove is present running from the posterior lip of the blastopore down the centre of the primitive streak. Three transverse sections through an egg of this stage are shown in figs. 5, 6, and 7. Fig. 5 passes through the blastopore at about the middle point of its length, where it is very clearly open; at this time it is about an eighth of the total length of the ovum. Fig. 6 passes through the region immediately behind the blastopore through the primitive streak and groove. Immediately beneath the primitive groove there is a small cavity bounded by the protoplasm of the primitive streak, the nuclei round it being arranged in a roughly columnar manner, and filled with very small yolk-spheres, among which are one or two nuclei; this cavity is marked *c* in the figure. It ends blindly in front and behind, and probably is homologous with the area which Mr. Sedgwick (1) calls the polar area in P. capensis, which, both in position and structure, it closely resembles, with the exception of the fact of its being filled with yolk-spheres in the New Zealand species. Fig. 7 passes through the posterior end of the primitive streak, where it is thinning out, and the groove is much shallower. These three sections bear a very close resemblance to figs. 25 and 26 of Mr. Sedgwick's second paper on the Cape species (1). The peripheral nuclei in the region of the blastopore and primitive streak have a more or less columnar form instead of lying flat against the side as they do over the rest of the ovum. The anterior part of the egg is enveloped in a single layer of flat nuclei.

In an ovum of a slightly later stage the blastopore has increased a little in length, the primitive streak is much larger and more marked, the nuclei being very closely packed, and the primitive groove is considerably deeper; the so-called polar area has disappeared. This stage is the latest which was present among the January eggs, except some quite old embryos which were almost ready for birth.

I have examined several series of sections of older embryos, i. e. in which they were developed, but have not thought it necessary to give an account of them, as the process of development seems to be similar to that of P. capensis described by Mr. Sedgwick (2).

The only point of interest in which it differs from that species is that the first somite (i. e. that of the præoral or antennal segment) opens by a duct to the exterior in precisely the same way and position as do those of the third to fifteenth segments, so proving it to be the nephridium of the segment with the same relations as those of the posterior ones. This is shown in figs. 10 and 11; in the former the opening of the duct to the exterior just outside the nerve-cord is shown, and in the latter, which is separated from the former by three sections, its opening into the somite. The probability of the nephridial nature of this somite was pointed out by Mr. Sedgwick.

Summary of the Results of my Investigations on the Development described in this paper and the previous one (4) published in vol. xxviii, part 2, of this Journal.

1. The ovum is heavily charged with food-yolk; the segmentation is on the centrolecithal type; the protoplasm is mainly at one pole of the egg, and in this protoplasm nuclei arise, probably by the division of the segmentation nucleus. The protoplasm forms a loose reticulum containing nuclei on the surface of the egg, which first extends over only a small area, but later spreads over the surface until, in the latest stage which I have, it covers about half the periphery of the egg.

2. In the latest segmenting ova there are small masses of protoplasm in the centre of the egg, which masses sometimes contain nuclei.

3. Shortly after the segmentation begins the yolk becomes divided up into a number of rounded segments, which, however, bear no relation to the true segmentation.

4. The central nuclei of those lying just beneath the periphery multiply much more rapidly than those over the rest of the ovum, thus coming to form a special area, which finally extends along about the middle third of the ovum, and consists of a loosely-reticulate mass of protoplasm containing a large number of nuclei, and having in transverse section an irregular triangular shape. Nuclei are present through the rest of the ovum, being more numerous near the periphery than the centre.

5. The triangular-shaped protoplasmic area becomes more compact and flattens itself out, forming a plate-like mass of protoplasm densely packed with nuclei on the surface of the middle third of the ovum. This plate is the blastoderm. The nuclei over the rest of the egg have undergone no change.

6. The blastoderm grows round the ovum till it covers about

one half of its surface, at which time it is thickest in the centre and thins gradually towards its edges.

7. The epibolic growth of the blastoderm continues until only a very small space in the middle of the ventral face of the ovum is left uncovered.

8. A proliferation of the nuclei behind the uncovered area in the middle line takes place, forming a (in transverse section) keel-shaped mass of nuclei extending along about the posterior half of the ovum. The nuclei at the sides of the space also proliferate.

9. The protoplasm round the space becomes inflected, and so forms a blastopore. The proliferating mass of nuclei or primitive streak increases in amount.

10. The blastopore increases in length considerably, and becomes more open. The primitive streak also becomes wider and deeper, and a groove—the primitive groove—appears along its centre. Beneath the primitive groove a small cavity filled with yolk and bounded by columnar nuclei, and apparently homologous with the polar area of P. capensis, appears.

11. The blastopore and primitive streak and groove increase and become more marked. The polar area disappears.

12. Up to this stage no trace of any cell-outlines is visible, but the protoplasm forms a syncitium, in which nuclei are irregularly scattered. At this point a large gap is present in my investigations.

13. A layer of yolk is present outside the embryo. This peripheral yolk becomes gradually absorbed, and various changes are undergone by the embryo (descriptions of which are given in (4), vide summary, p. 230) until it reaches the stage at which the absorption is complete, when the appendages begin to appear, &c.

14. The later development, i.e. after the appendages are formed, is similar to that of P. capensis, the only interesting point of difference being that the duct of the first somite opens to the exterior.

General Considerations.

The investigations which I have made on the January eggs of Peripatus novæ-zealandiæ, although the stages examined were few, nevertheless throw a good deal of light on the subject of the early history of the development. In my former paper (4) I remarked upon the strange dissimilarity which existed from the segmentation stages up to quite late ones between the three species of Peripatus whose developmental history has been at all fully worked at. In the cases of P. capensis and P. novæ-zealandiæ at all events this remark now requires modification. The developmental history of the latter is now fairly complete as far as the gastrula stage, and up to that point its resemblance to that of P. capensis is very marked. As I pointed out before (4) the segmentation is very similar, the main differences being easily accounted for by the presence of the yolk in the one species, and its almost total absence in the other. I have now shown that in the New Zealand species the ectoderm, which at first covers only a portion of the ovum, gradually grows round until only a small space on its ventral side remains uncovered, and at this spot an invagination takes place forming the blastopore, behind which in the middle line the primitive streak and groove are present. In all these stages the resemblance to the corresponding ones of P. capensis is very striking, the main difference consisting, as in the segmentation stages, in the presence of the yolk. This similarity is clearly seen on a comparison of the figures in Mr. Sedgwick's paper (1) and my own (4). In fact it seems somewhat strange that the almost total loss of the yolk, which must almost certainly have been possessed originally by the Cape species, should have apparently been accompanied by so few modifications in its development, since so important a change of conditions might have been expected to exert a considerable influence on the latter.

Unfortunately there are many stages wanting between the gastrula stage and the next one which I have described in my previous paper (4). In it one of the most remarkable features was the presence of the yolk outside the embryo, between it and the vitelline membrane. It might be more correct and intelligible to consider this as ectodermic yolk. In P. capensis protoplasmic strands are present, passing from the ectoderm to the egg-shell, especially in the region of the dorsal hump, and these very probably indicate that ectodermal yolk was present at one time in this position. In his last paper (5) on the development of the Cape species, Mr. Sedgwick states that the ectoderm is much vacuolated and contains globules which he believes to be yolk up to a comparatively late stage of development. Thus it seems probable that both species were possessed of ectodermal yolk. In the gastrula stage in both species there is no sign of any trace of yolk which probably therefore arises later. In P. novæ-zealandiæ this yolk is so thick that it completely obscures the external characters, which cannot be made out in surface view till the stage at which the appendages are forming when the ectodermal yolk is almost completely absorbed. As to the mode and time of origin of this ectodermal yolk in P. novæ-zealandiæ I am not able to make any statement, as in the youngest egg in which it is present it is already well formed, and constitutes a very thick layer; and I do not know whether it is derived in some way from the central yolk, or whether it arises as a fresh formation in the ectoderm cells. However, the fact that in both species it is absent in the gastrula stage and appears later seems to point to its being an ancestral feature in the development. This, as well as many other points of interest in the development of this interesting species, will unfortunately have to remain unexplained until someone shall be fortunate enough to obtain embryos of the intermediate stages.

Summary of Dates of Embryos which are figured in this paper and the previous one (4).

Previous paper (4):

Figs. 1—10.—December. Figs. 11—20.—April. Figs.

21 *a, b, c.*—July. Fig. 22.—July. Fig. 23.—December. Fig. 24.—December. Fig. 25.—July. Fig. 26.—July.

This paper:

Figs. 1—9.—January. Fig. 10.—July. Fig. 11.—July.

Thus, speaking generally, the ages of the embryos received in the various months are:

December.—Stages from unsegmented ova up to that at which nuclei were present at intervals just beneath the surface round about half the ovum.

January.—From late segmentation up to gastrula stage.

April.—Two embryos showing the beginning of the formation of the blastoderm, and also several stages with ectodermal yolk.

July.—Stages in which the appendages are being formed up to embryos which were ready for birth. There were also newly-born young.

Conclusion arrived at as to Time of Development.

Probably the ova pass from the ovary into the uterus in December, and the young are born in July, the development thus occupying a period of about eight months.

This, though apparently usually the case, cannot be universal since in each lot there were one or two females which contained embryos ready for birth, and also the embryos in one female vary somewhat in age.

This statement as to the period of gestation has already been made by Mr. Sedgwick (3).

List of Papers referred to.

(1) Sedgwick, A.—"The Development of the Cape Species of Peripatus," Part II, 'Quart. Journ. Micr. Sci.,' vol. xxvi.

(2) Sedgwick, A.—"The Development of the Cape Species of Peripatus," Part III, 'Quart. Journ. Micr. Sci.,' vol. xxvii.

(3) Sedgwick, A.—"A Monograph of the Species and Distribution of the genus Peripatus," 'Quart. Journ. Micr. Sci.,' vol. xxviii.

(4) Sheldon, L.—"On the Development of Peripatus novæ-zealandiæ," 'Quart. Journ. Micr. Sci.,' vol. xxviii.

(5) Sedgwick, A.—"The Development of the Cape Species of Peripatus," Part IV, 'Quart. Journ. Micr. Sci.,' vol. xxviii.

EXPLANATION OF PLATES XXV & XXVI,

Illustrating Lilian Sheldon's paper, "On the Development of Peripatus novæ-zealandiæ."

List of Reference Letters.

Bl. Blastoderm. *Btp.* Blastopore. *c.* Cavity, corresponding to polar area of P. capensis. *Pm. A.* Protoplasmic area. *Pr. Gr.* Primitive groove. *Pr. St.* Primitive streak.

All the figures were drawn with Zeiss's camera lucida; Figs. 3 *a* and 9 were drawn under Zeiss's oc. 2, obj. CC; Fig. 4 under Zeiss's oc. 2, obj. A; and the rest under Zeiss's oc. 2, obj. B.

Fig. 1.—Transverse section through an ovum, in which the blastoderm has grown nearly half way round the yolk.

Fig. 2.—Transverse section through the centre of an ovum, in which the yolk is nearly covered by the blastoderm.

Fig. 3.—Transverse section through an ovum, in which the primitive streak is beginning to arise.

Fig. 3*a*.—Transverse section through the portion of the same ovum which is not covered by the blastoderm, drawn under a higher power.

Fig. 4.—Transverse section through the centre of a young ovum before the formation of the blastoderm, showing the multiplication of the nuclei in one region near the periphery.

Figs. 5, 6, and 7.—Three transverse sections through an ovum in which the blastopore is well formed.

Fig. 5. Through the blastopore.
Fig. 6. Just behind the blastopore.
Fig. 7. Near the posterior end of the primitive streak.

Fig. 8.—Transverse section through an ovum with a primitive streak.

Fig. 9.—Transverse section through a portion of the same ovum, to show the invagination at the blastopore beginning at the anterior end of the primitive streak. Drawn under a higher power than Fig. 8.

Fig. 10.—Transverse section through an embryo with appendages, to show the duct of the first somite opening to the exterior.

Fig. 11.—Transverse section through the same embryo four sections posterior to Fig. 10, to show the duct opening into the first somite.

Fig 1.

Fig. 2.

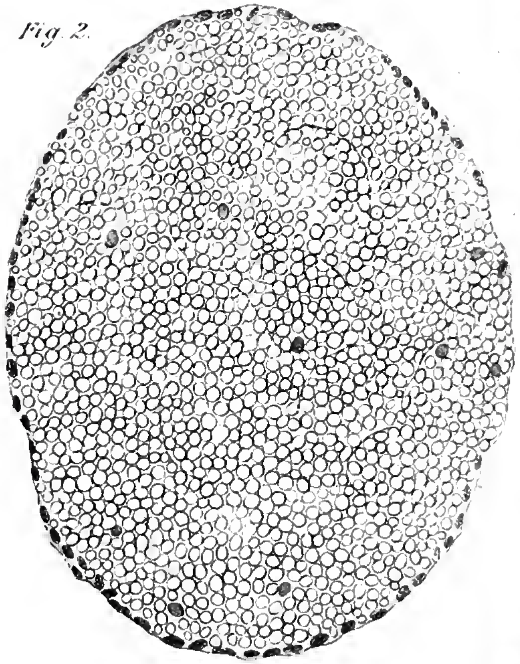


Fig. 4.

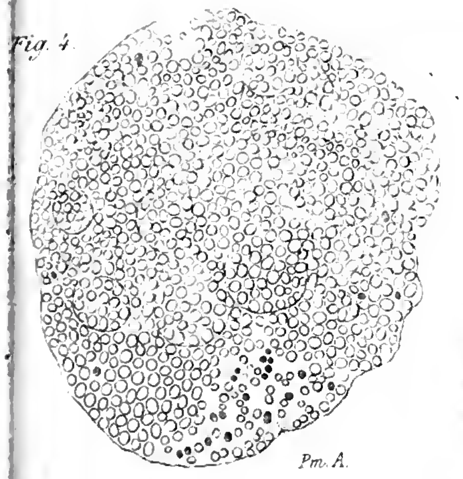


Fig. 3.

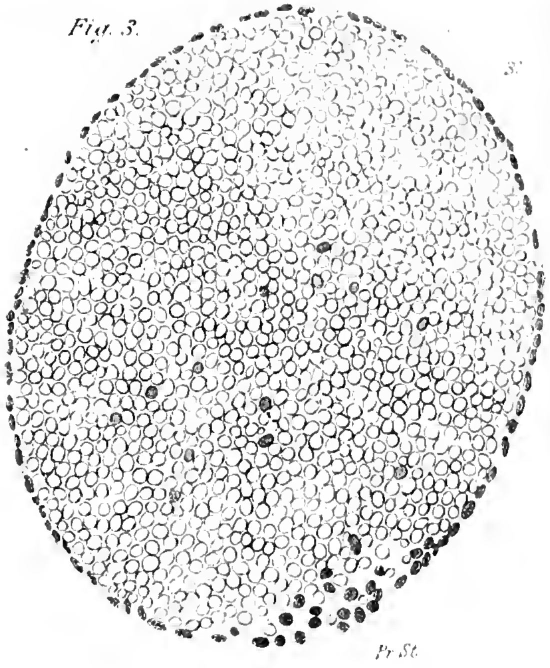


Fig. 3 a.

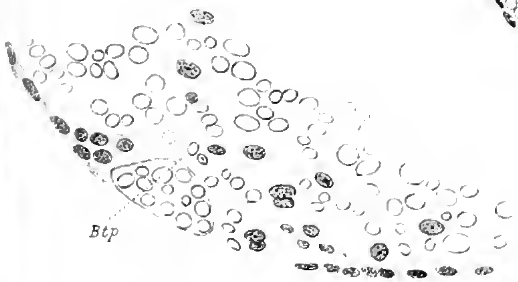


Fig. 5.

Fig. 6.

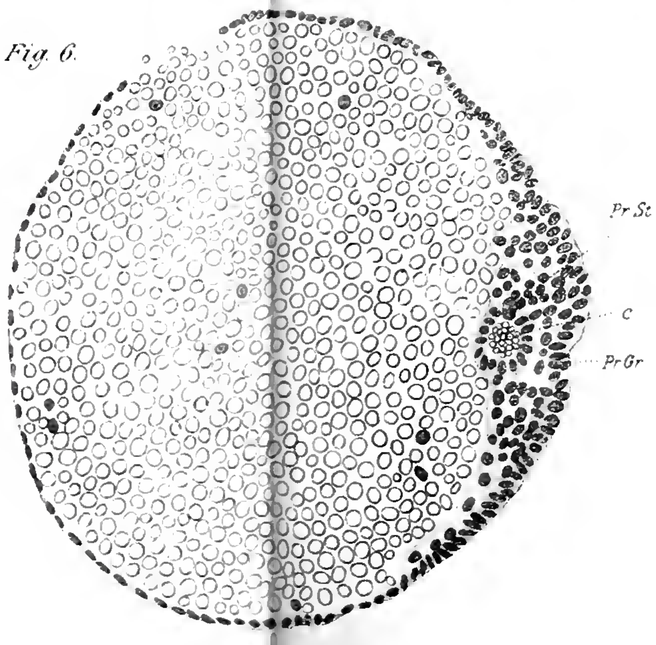
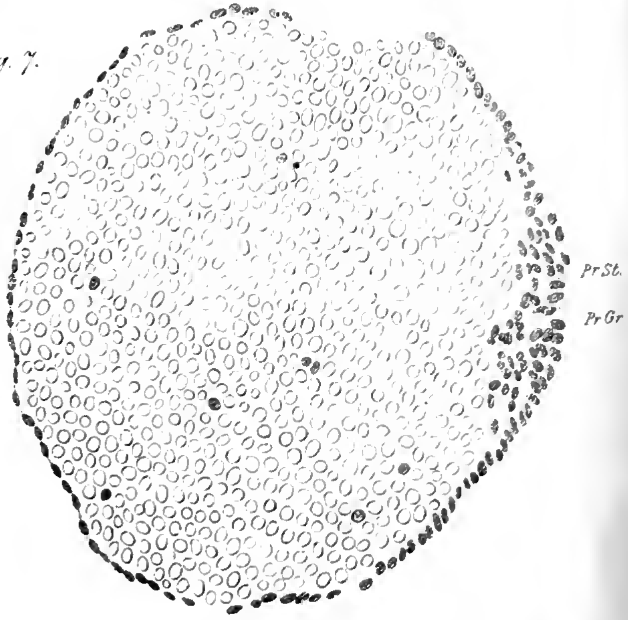


Fig. 7.



F. Huth, Lith^r Edin^r

Fig. 8.

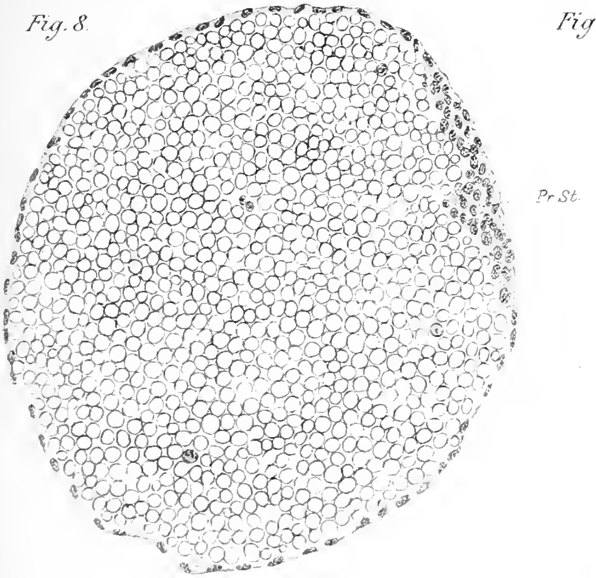


Fig. 9.

Fig. 10.

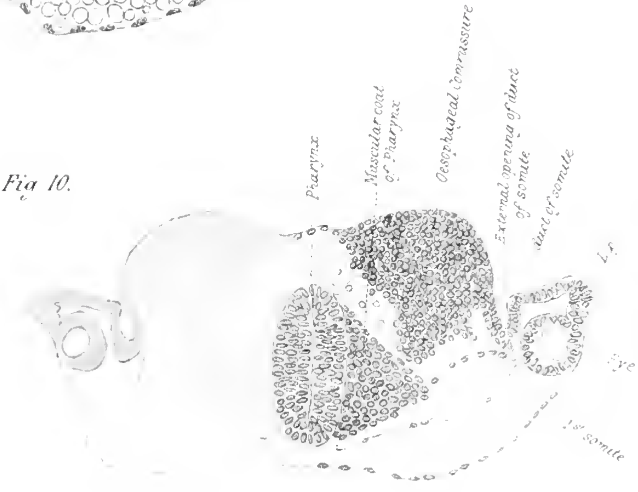


Fig. 11.

F. Huth, Lith^r Edin^r

Note on the Development of Amphibians, chiefly concerning the Central Nervous System; with Additional Observations on the Hypophysis, Mouth, and the Appendages and Skeleton of the Head.

By

Henry Orr, Ph.D.,
Princeton, New Jersey.

With Plates XXVII, XXVIII, and XXIX.

The material for the investigations which are described in this article was collected at Princeton, N.J., except a few specimens of Triton alpinus kindly given me by Professor H. F. Osborn. Through a failure to obtain adult specimens at the time when I obtained the embryos, there remains room for doubt as to the exact species of the embryos. The Amblystoma embryos correspond exactly to Clarke's[1] description of the embryos of Amblystoma punctatum, but there is one difference in the appearance of the egg-membranes which leads me to think that this may be a different species from that described by Clarke. It is, perhaps, A. bicolor, for which Jordan[2] gives only the habitat New Jersey. The Frog embryos are either Rana halecina or R. palustris. I judge them to be the former. In the stages of development with

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[1] S. F. Clarke, "Development of Amblystoma punctatum, Part I, External," 'Studies from the Biological Laboratory of the John Hopkins University," No. ii, 1880.

[2] D. S. Jordan, 'Manual of the Vertebrates of the Northern United States, &c.,' 1876.

which my work has dealt there are probably no specific differences in the embryos.

The developing eggs of this species of Amblystoma seem to present a remarkable case of symbiosis. The eggs, surrounded by their gelatinous matrix, appear as a white mass floating on the surface of the water. (I found them in a small swampy pool on elevated ground.) In the first lot that I collected the medullary plates were just forming, and the two membranes surrounding each egg appeared perfectly homogeneous and transparent. In the second lot, collected some days later, the embryos were somewhat elongated, and the medullary canal had apparently just closed. In this lot the internal membrane of each egg was coloured a uniform light green by the presence in the membrane of a large number of minute globular green Algæ. Neither in the spaces adjoining the internal membrane, nor in the external membrane, nor in the matrix, was there any colouration or trace of this Alga. The external membrane was transparent and the matrix white and translucent as before. In a third lot, collected when the balancers and gills had appeared, these conditions were the same, except that the Algæ had increased in number and the colour was a much darker green. I have not discovered how the Algæ enter the membrane, nor what physiological effect they have on the respiration of the embryo, but it seems probable that in this latter respect they may have an important influence.

Clarke has given a detailed description of the external appearance and changes of the embryo of Amblystoma punctatum, so that for this part I may refer the reader to his work. As might have been expected, Amblystoma and Triton present much similarity in their development, while both differ in about the same degree from the Frog. The chief points of which I shall treat are the central nervous system, the hypophysis, and some other parts and appendages of the head. The comparison of the embryos of the different groups affords some light in the attempt to explain the development of some of the more complicated parts. In order to avoid repetitions I have not separated the descriptions of parts which are intimately related to each other in the process of their development. Much of what I have written will have been readily inferred by embryologists, though the embryology of the genus on which most of my work is based has not hitherto been worked out. But as some of my conclusions are different from those previously expressed, I have thought best to give in detail a description of the facts that the reader may thereby test my conclusions.

The first differentiation of the central nervous system of Amblystoma appears as figured in the sagittal and transverse sections (figs. 1, 2 A, 6 A). The transverse section is cut through the middle dorsal region. By the thickening of the dorsal epiblast there are formed two broad epiblastic plates (*M. P.*), connected with each other on the median line by a thinner portion of epiblast. A slight longitudinal groove (*G.*) is formed by the sinking inward of this thinner median portion of epiblast. Directly underneath this groove there is a longitudinal fold in the hypoblast, which causes a conspicuous median groove in the roof of the alimentary tract. The dorsal part of this hypoblastic fold touches the epiblast along the median line; and the part adjacent to the epiblast is the part which later forms the notochord. On each side of the hypoblastic fold, and apparently fused with it, lie the two layers of the mesoblast (*So.*, *Sp.*). An examination of all my sections shows that the condition of the mesoblast at this point is the same in Amblystoma as Hertwig discovered it to be in Triton.[1] Some of my sections show a space between the two layers of mesoblast continuous with the archenteron. I have not found any trace, however, of mesoblast originating from any other part of the hypoblast or from the yolk.

The sagittal section (fig. 1) passes through the epiblastic groove (*G.*) and the dorsal groove in the hypoblast, thus cutting only the thin median part of the epiblast and the hypoblast. The sections on either side of this median section pass through the thicker part of the body wall, which contains also the

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[1] For a statement of Hertwig's results, see A. C. Haddon, 'An Introduction to the Study of Embryology,' 1887.

mesoblast. In section, fig. 1, it may be seen that the thinner epiblast in the median line does not extend to the extreme anterior end of the rudiment of the nervous system, but that it ceases in the head region, while anteriorly the lateral medullary plates unite with each other undiminished in thickness, thus forming an anterior medullary plate (*a. M. P.*). The distinction between anterior and lateral plates is arbitrary and adopted only for convenience. They might be described as one thickened epiblastic plate, bent in such a manner that the curved part lay in the head region, while the two straight parallel ends lay one on each side of the dorsal median line. The distal periphery of the anterior medullary plate is a curve. Fig. 6 A represents a section through the anterior plate of the same embryo from which fig. 2 A was taken. It may be seen here that there is no sign of a bilateral division of the neural rudiment at its anterior end.

The further development of the medullary plates in the dorsal region is shown in figs. 3 B, 4 C, 5 D, Pl. XXVII. The lateral edges of the plates roll slightly upwards, forming the folds (*M. F.*). At the same time the median edges become pressed together, thus causing the floor of the median groove (*G.*) to sink farther inwards. The space between the medullary folds (*M. F.*) gradually decreases in size as the folds approach the median line. There is no very marked increase in the height of the folds. The originally dorsal surfaces of the medullary plates, bending inward, become pressed together in a vertical median plane under the groove, *G.* Across this line of median vertical contact there is no fusion of the cells. A heavy pigment marks this line (*g.*, fig. 5 D) as continuous with the pigmented surface. Beneath the lower extremity of the line *g.* a small ridge of cells, continuous with the lateral halves of the neural rudiment, marks the original median connection of the medullary plates. By a comparison of the figures illustrating this period of development it may be seen that the cells of the neural rudiment gradually become smaller (owing to division and loss of yolk), that the whole organ becomes more compact and occupies much less space in the end than in the beginning. The primarily broad space enclosed laterally between the medullary folds (*M. F.*) diminishes in size until it becomes a small rounded groove in the dorsal part of the neural rudiment, as represented at fig. 5 D. In a section through the cervical region of the same embryo (fig. 10 D) the epiblast has met above the groove, thus forming a relatively very small neural canal. As the epiblast of the two sides fuses above the canal the lumen of the latter becomes in some places suppressed, leaving as its only remnant a heavy accumulation of pigment.

In the species of Frog examined by me the lumen of the neural canal at this period of development becomes suppressed throughout the posterior part, thus differing in this respect from Goette's account of Bombinator. Towards its posterior extremity the neural rudiment of the Frog closely resembles that of an osseous fish at the same period. This manner of development of the neural rudiment in Amphibians presents a stage intermediate to the condition of Elasmobranchs and Reptiles on the one hand and the condition of Petromyzon and the Teleosts on the other.

After the fusion of the epiblast dorsal to the neural rudiment the neural canal opens from before backwards along the pigmented line (*g.*, fig. 5 D) which has previously been described. The canal, at first somewhat irregular, becomes in cross-section dorso-ventrally elongated. The walls of the neural tube become bilaterally symmetrical, and are thickest laterally. A transverse section through an older embryo of Amblystoma (fig. 11) shows the result of these changes. In the Frog embryo the appearance is fundamentally the same.

In the cephalic region the development of the neural rudiment differs from that in the dorsal region. In order to clearly understand this difference, it is necessary to bear in mind that the anterior medullary plate (*a. M. P.*, figs. 6 A, and 7 B) is not a paired continuation of the dorsal medullary plates, but is a transverse curved plate connecting the two dorsal plates. It is also necessary to distinguish the modifications caused by the cranial flexure, in order to recognise the homology between the parts in the dorsal and cephalic regions. It will be seen in the sagittal section (fig. 1) and in the transverse section (fig. 6 A) that at first the anterior medullary plate (*a. M. P.*) is externally flattened. In fig. 7 B, where the dorsal medullary folds have appeared (compare fig. 3 B), the lateral edges of the anterior medullary plate turn slightly upward (where the same letters are affixed to the numbers the sections are from the same embryo). In fig. 8 C this upward bending of the lateral edges has increased, and in fig. 9 D the edges meet dorsally. During this process the median part of the anterior medullary plate (*A. F.*) departs from its original slanting position (fig. 1), and comes to lie nearly parallel to the dorsal surface of the embryo, though at a lower level. The floor of the dorsal medullary groove extends forwards nearly horizontal as far as the region of the mid-brain; there it bends downwards almost at a right angle, and joins the posterior edge of the medially horizontal anterior plate. Thus is formed the primary cranial flexure before the medullary folds have fused above the neural canal. In the head this fusion takes place later from behind forwards, curving down to the anterior edge of the anterior medullary plate (*A. F.*, fig. 9 D). The cranial flexure therefore is not simply a bend in the floor of the primitive neural tube, but is also a bend in the dorsal surface. It involves the anterior part of the neural tube in a bend about equal to a right angle. The line of fusion of the medullary folds in the head is homologous with the same fusion in the dorsal region. The morphologically dorsal surface of the neural tube extends therefore throughout the region of the fusion to the anterior edge of the anterior medullary plate. Taking into account the anterior bending of the axis of the neural tube, its morphologically anterior surface would be represented by the anterior medullary plate, which extends from the above-mentioned vertical portion of the floor to the anterior end of the dorsal fusion.

The anterior medullary plate of Amblystoma is homologous with the anterior medullary fold of the Lizard, and for the purpose of indicating this homology I have marked it in the drawings as the anterior medullary fold. In both cases it forms the primitive morphologically anterior surface of the brain. There is a marked difference between this anterior brain-surface in the Lizard and the same part in Amblystoma. In the Lizard the anterior brain-surface comes to lie at a right angle to the axis of the dorsal part of the neural tube, and faces posteriorly; in Amblystoma it lies parallel to the axis of the dorsal part of the neural tube, and faces ventrally. This difference seems to be due to the different methods according to which in the two forms the medullary folds unite to form the medullary tube. In Amblystoma the condition is caused in the following manner. In the primitive neural rudiment there is a thinner median portion of epiblast lying between the dorsal medullary plates and behind the anterior medullary plate. As the distal lateral edges of the neural rudiment approach each other different effects are produced in the region of the thin median epiblast and in the anterior plate. In the first-named region, as the lateral edges of the medullary plates approach each other, their median edges are compressed, and as the width of the neural rudiment decreases its median thickness increases. In the anterior plate there is no thin median portion and no thickening resulting from compression, therefore as the lateral edges approach each other the median portion must bend downward. In this manner the median portion of the anterior plate comes to lie at a much lower level than the floor of the neural tube in the dorsal region. The cranial flexure is the result of the presence of an anterior medullary plate, and, as I have elsewhere pointed out, this seems to be the case also in the Lizard.

In the Frog the anterior medullary plate forms a fold directly comparable to the medullary folds in the dorsal region. The anterior fold is, however, much more prominent than the folds in the dorsal region. Fig. 19 represents a median sagittal section of a Frog embryo at this stage. The lateral sections of this embryo show that the anterior fold (*A. F.*) is laterally and posteriorly continuous with the paired medullary folds, thus enclosing anteriorly and laterally the anterior enlargement of the neural groove (*F. B.*). This anterior enlargement is the first rudiment of the vesicle of the fore-brain. The cranial flexure in this embryo is in process of formation; when the medullary folds in the head later meet dorsally, the cranial flexure is complete. The presence of an elevated anterior fold in the Frog, and its absence in Amblystoma, is not so much due to absolute difference in the form of the neural rudiment as to the relative growth of the surrounding parts. In Amblystoma the presence of the hypoblast and anterior end of the alimentary tract beneath the anterior medullary plate (fig. 9 D) prevents the latter from appearing as a fold raised above the head surface. But at a later period the hypoblast disappears from beneath the anterior plate, and the external surface of the anterior plate is then covered only with epiblast (fig. 12 E).

The disappearance of the hypoblast and alimentary cavity from beneath the anterior medullary plate, or rather the (morphologically) anterior surface of the brain, is due to the more rapid growth of the brain, especially an increase of length, by which the fore-brain advances to a position in front of the anterior end of the alimentary cavity. At a very early stage the anterior end of the alimentary cavity is enclosed only by hypoblast and epiblast (*Ep.*, *Hyp.*, fig. 1). A fusion of these two layers soon takes place at this point, and indicates the eventual position of the mouth-opening. As the fore-brain is projected anterior to this mouth-fusion, the epiblast dorsal to the fusion is brought into close contact with the anterior surface of the brain (fig. 12 E). Figs. 12 E and 13 E represent two nearly sagittal sections of the same embryo, one section passing through the oral fusion and hypophysis-rudiment, the other passing through the notochord and pineal rudiment. The age and general condition of development of this embryo will be best understood by comparing these sagittal sections with sections 14 F, 15 F, 16 F, which are horizontal and taken from an embryo of the same age. The anterior part of the alimentary canal is distended into a large pharyngeal branchial cavity (fig. 12 E). The hypoblast of the anterior wall of this cavity touches the nearly vertical floor of the fore-brain which forms the wall of the infundibulum. The lower anterior wall of the pharyngeal cavity is fused with the epiblast at *M.*, forming the oral fusion. A wedge-shaped mass of epiblast (*Hph.*) extends inward between the oral fusion and the wall of the infundibulum; this is the rudiment of the hypophysis. It is not necessary to interpret this condition as an ingrowth of the epiblast. I am inclined to think that the wedge-like shape of the epiblastic mass is due to the pressure of the more rapidly growing brain. It is evident from this section that at this stage of the development of Amblystoma there is no appearance of a stomodæum or epiblastic mouth-cavity. From this time on the rudiment of the lower jaw begins to extend forward, and grows beyond the oral fusion and hypophysis toward the nasal tip of the head. The epiblast retains its connection with the hypoblast, and also for a time with the hypophysis; thus the epiblast posterior to its point of fusion with the hypoblast is pressed close against the epiblast anterior to the point of fusion. These two united layers of epiblast form an apparently solid mass extending from the hypoblast to the surface of the head (*M.*). This stage is illustrated in the nearly median sagittal section, fig. 17 G. The hypophysis (*Hph.*) has broken loose from the in-folded mass of epiblast, and still remains adjacent to the posterior wall of the infundibulum (*In.*). The point for the ultimate external opening of the mouth (*M.*) has been moved by the growth of the lower jaw, forward to a position anterior to region of the optic chiasma (*Ch.*). The position of the perfected mouth-opening is shown in fig. 18. The condition of the rudiment of the mouth, as represented in fig. 17 G, is that which has been described by other writers as a solid ingrowth of epiblast or a stomodæum; but it is evident from the above-described manner of development that the term ingrowth leads to a false conception as to the origin of the part referred to. The primary development of the hypophysis, and the growth forward of the lower jaw, are fundamentally the same in Amblystoma as I found them in the Lizard.

During the process above described, the parts of the brain and the hypophysis and notochord change their positions with relation to each other. Fig. 13 E shows the anterior end of the notochord, which in this embryo is at some distance from the hypophysis, while the floor of the hind-brain (*H. B.*) is widely separated from the infundibulum. There is a median thickening of the hypoblast extending from the anterior end of the notochord down to the hypophysis. This thickening seems to disappear very quickly after formation. It seems possible that this median thickening may be homologous with that foremost part of the notochord which in the Lizard and in the Mole extends as far as the epiblast at the hypophysis. In the Anura at an early stage there is a layer of mesoblast extending across the median line between the anterior end of the notochord and the hypophysis-rudiment. Why the mesoblastic product of the hypoblast along the median line at this region does not become differentiated into notochord in the Amphibia, as it does in the Lizard and the Mole, may be explained perhaps by the changes which immediately succeed this stage—changes which would be hindered by a developed notochord in this region. The changes thus referred to are exhibited in fig. 17 G. Here the secondary cranial flexure has appeared in the hind-brain, and the floor of the hind-brain is pushed against the infundibulum, causing the latter to be slightly compressed. At the same time the bending floor of the hind-brain has pushed the notochord downward, so that the anterior end of the developed notochord touches the hypophysis. (These changes of position are of course to be understood only in terms of relative topography as the absolute changes of location cannot be ascertained. Thus, the changes might be accounted for by supposing the secondary cranial flexure to lift the anterior part of the brain and head upward; but the former view lends itself more readily to the explanation of the facts, and admits of more extended homologies).

As nearly as can be judged from the more limited number of my specimens of Triton, the method of development during the above-described stages is exactly the same in Triton as in Amblystoma; though I should add that my youngest stage of

Triton corresponds with the stage of Amblystoma represented in figs. 12 E to 16 F. From this stage onward my series of the embryos of the two genera run about parallel, and a great similarity continues to exist throughout all the stages which I have examined.

The development of the hypophysis and mouth in the Frog differs in a marked manner from the development of the same organs in Amblystoma and Triton. The same fundamental principles seem to obtain in both methods of development, but the difference is apparently due to a different proportional rate of growth of the parts adjacent to each other. The development of these parts in the Frog is illustrated in figs. 19—23. These sections are sagittal, or nearly sagittal, and all meet the median vertical plane in the centre of the mouth-fusion. In fig. 19, between the lip of the anterior medullary fold (*A. F.*) and the mouth-fusion, lies the epiblast which is to form the hypophysis. In this embryo the cranial flexure is not yet complete, and the alimentary cavity extends forward beyond the anterior fold. The rudiment of the hypophysis lies therefore immediately exterior to the anterior fold. In a somewhat older embryo (fig. 20) the brain is enclosed, and has increased so much in size that it projects forward anterior to the mouth-fusion (*M.*). The increase of the cranial flexure has caused a change in the position of the anterior fold. In fig. 19 the anterior fold occupies a vertical position, and in fig. 20 it occupies a horizontal position (*A. F.*), forming in both cases the morphologically anterior wall of the brain. In embryos slightly younger than the one represented by fig. 20 serial sections show that the dorsal linear opening of the central nervous system extends as far as the horizontal anterior fold to about the point indicated by *o. g.* in fig. 20. When this opening becomes closed by the dorsal median fusion of the lateral walls, the line of fusion remains marked by the accumulated mass of epidermoidal pigment. This pigmented line is cut at *o. g.* in fig. 20, very near the end which indicates the boundary of the anterior fold. It may be seen from the figures that the change of position of the anterior fold is accompanied by a corresponding change in the position of the hypophysis rudiment (*Hph.*), so that the latter continues in the same topographical relation to the anterior fold. The rudiment of the hypophysis extends a short distance posterior to the limit of the anterior fold (*o. g.*).

The next three stages (figs. 21, 22, 23) illustrate the further development of these parts. The most striking changes are the increase of the cranial flexure and the growth of the dorsal part of the fore-brain. (This latter is not so well shown in fig. 21 owing to the obliquity of that section.) It is evident that these changes would cause a relative change of position of the point marked *o. g.* in fig. 20. In two of the sections (figs. 22, 23) may be seen a slight groove (*o. g.*) in the morphologically anterior surface of the brain. This groove lies at first between the optic stalks, and ultimately just anterior (or morphologically dorsal) to the chiasma. I have not been able to absolutely demonstrate that the groove (*o. g.*) is developed from the point *o. g.* in fig. 20, but the evidence in favour of the view that such is the case seems to me so strong that I have been forced for the present to accept that conclusion. In the Lizard the primitive opening of the brain extends down the anterior surface of the brain to a point between the optic stalks, and in the Lizard there is also a similar groove at that point. In the present case we have only to imagine that owing to the increase of the cranial flexure and the growth of the fore-brain the point *o. g.*, fig. 20, has receded relatively in a posterior direction, until it reached the point *o. g.*, fig. 23. In figs. 22 and 23 such a relative posterior recession of the groove *o. g.* is perfectly evident. This relative recession is due chiefly to the greater growth in the region in front of the point *o. g.* It will be seen that in all these five embryos (19—23) the posterior end of the hypophysis-rudiment lies at about the same distance behind the region of the point *o. g.*, but the lower jaw advances continually until it extends anteriorly beyond the posterior end of the hypophysis and beyond the point *o. g.* This process of growth is essentially the same in the Frog as in Amblystoma and Triton; but in the Frog the growth of the dorsal part of the fore-brain and the growth forward of the lower jaw take place at the same time, and in nearly the same extent, thus making the hypophysis appear as an ingrowth, whereas it is simply that part of the epiblast which has retained its original position with relation to the brain, and which has become surrounded and embedded by the expansion of the adjacent parts. There is another point of difference between the hypophysis of the Frog and the hypophysis of the Urodele embryos. In Amblystoma and Triton the hypophysis at the very beginning of its differentiation lies immediately adjacent to the posterior wall of the infundibulum, and later the anterior end of the notochord touches its posterior side. In the Frog the hypophysis at first does not reach the posterior wall of the infundibulum. As it begins to loose its connection with the epiblast it gradually comes to lie nearer the posterior wall of the infundibulum, and finally lies slightly ventral to the anterior end of the notochord, the latter being pressed against the infundibulum. Thus a nearly similar condition results from two apparently different methods of development. In Amblystoma the position of the hypophysis is the result (mechanically) chiefly of a forward movement of the anterior part of the brain. It seems most probable that the case is the same in the Frog, but that the forward movement of the anterior part of the brain takes place at a later date.

To Goette's[1] description of the other parts of the brain of Anura during these stages I have nothing to add. There are a few points, however, which may be mentioned for the sake of orientation as to the stages of development of the embryos here referred to. In a transverse section through the head of an embryo at the stage of fig. 20 the lumen of the fore-brain appears triangular, with one angle representing the dorsal crest of the brain, and the side opposite that angle representing the morphologically anterior wall of the brain. The lateral angles of the lumen are the beginnings of the optic outgrowths. In an embryo at the stage of fig. 21 the optic outgrowths are somewhat prolonged, and the lumen is drawn out laterally in

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[1] Goette, 'Die Entwickelungsgeschichte der Unke,' Leipzig, 1875.

them. In the embryo of fig. 22 the optic outgrowths are bent backwards and upwards, and in the embryo of fig. 23 the eye has progressed so far that the lens has appeared.

In the Amblystoma embryo of series D, in which the fore-brain is not yet enclosed, there is no trace of the optic vesicles. The next older stage of Amblystoma among my specimens is illustrated in figs. 12 E—16 F. The condition of the cranial flexure is shown at 12 E. In the anterior wall of the brain may be seen the optic groove (*o. g.*), and behind the latter is the anterior fold (*A. F.*). Immediately posterior to the anterior fold is the rudiment of the infundibulum. At this stage the primary triple division of the brain is not yet very pronounced, and there is no trace of nerve-fibres in the brain. The position of the rudiment of the epiphysis (*Eph.*, fig. 13 E) indicates the posterior extent of the primary fore-brain. In fig. 16 F the fore-brain is represented in section parallel to its morphologically anterior surface very near the latter, and in the region of the optic stalks (*Ey.*). In this section the lateral thickenings of the brain wall in front of the optic stalks are the rudiments of the corpora striata, which appear much earlier in Amblystoma than in the Lizard. Fig. 15 F represents a horizontal section of the embryo passing through the dorsal part of the pharyngeal cavity and through the mid-brain above the region of the infundibulum. This section shows the rudiments of the eyes (*Ey.*), which as yet possess no lens. Fig. 14 F represents a horizontal section through the hind-brain and dorsal medulla. This section shows the rudiments of the fifth, seventh and eighth, ninth and tenth cranial nerves. In three places the hind-brain shows a marked dilation of its lumen, and the lateral walls of the brain pass around these dilated parts undiminished in thickness. Opposite these dilated parts of the lumen arise the three chief nerve-roots of the hind-brain. The most anterior dilation corresponds to the fifth nerve-root (*n. V*). The next dilation corresponds to the common root of the seventh and eighth nerves (*n. VIII* and *VII*), and the posterior dilation corresponds to the root of the tenth nerve (*n. X*). The rudiment of the ear (*E.*) lies between the regions of the posterior and middle dilations, and immediately behind the ear arises the root of the ninth nerve (*n. IX*). These dilated parts of the hind-brain in Amblystoma resemble in some degree what I have described as the neuromeres in the hind-brain of the Lizard, except that in Amblystoma they are fewer in number, and certain intermediate neuromeres appear to have been suppressed. I am inclined to think that the large quantity of yolk present in these parts in Amblystoma has considerably changed their appearance and development. These dilations of the hind-brain have disappeared in Amblystoma, as in the Lizard, by the time the nerve-fibres of the brain have appeared. It will be seen in fig. 14 F that the cranial nerves meet and fuse with the epiblast. This fusion I think corresponds with what has been described by Miss Johnson and Miss Sheldon[5] as the first or dorsal fusion of the cranial nerves with the epiblast. These authors have described this fusion for the fifth, seventh, and ninth nerves, and supposed it for the vagus. My section shows the correctness of their supposition. The vagus retains for some time this fusion with the epiblast, and from the point of fusion there soon grows posteriorly a large linear thickening of the epiblast, which forms the lateral nerve. This in its earlier stage is very conspicuous, but soon becomes much smaller. I have not been able to trace the different steps between what the above-named authors have called the "first (dorsal) fusion" and the "second (ventral) fusion." One of my series of sections of Triton alpinus shows the condition described by them as the "second (ventral) fusion." In this series the distal ends of the two primary branches of the fifth nerve touch the epiblast and appear to be fused with the same.

The further development of the brain is shown in figs. 17 G and 18. The irregular appearance of these sections is due to the fact that they are neither exactly median nor exactly vertical; they cross the median vertical plane in a line drawn through the epiphysis (*Eph.*) and the region of the optic chiasma (*Ch.*)

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[1] Johnson and Sheldon, "Notes on the Development of the Newt (Triton cristatus)," 'Quart. Journ. Micr. Sci.,' vol. xxvi, N. S., 1886.

and hypophysis (*Hph.*). The morphologically anterior surface of the brain has remained in about the same position that it occupies in fig. 12 E, but the floor of the hind-brain is bent downward and is pressed against the infundibulum. Just anterior to the epiphysis (*Eph.*) is a deep fold, extending transversely across the dorsal wall of the brain, and thus dividing off the secondary fore-brain. There is another longitudinal and median fold, extending from this transverse fold forward to the anterior surface of the brain; thus dividing the secondary fore-brain into the two hemispheres. This longitudinal fold is not so deep as the transverse fold. Fig. 35 represents a section transverse to the long axis of an embryo of the same stage as fig. 17 G. This section is behind the deepest extent of the median longitudinal fold, but still shows the transverse fold. The rudiments of the corpora striata, which are already evident at the stage of fig. 13 E, *st.*, are shown again in transverse section in fig. 35. The corpora striata extend parallel to each other on each side of the median line, along the morphologically anterior surface of the brain, and are limited ventrally by the optic groove (*o. g.*, fig. 17 G). Immediately ventral to the optic groove is seen the remnant to the anterior fold, containing a bundle of transverse nerve-fibres, of which a part form the optic chiasma (*Ch.*). In an exactly median vertical section of the brain of an embryo at the stage of fig. 17 G, this remnant of the anterior fold would be the thickest portion of the brain wall, being about as thick as the lateral walls of the medulla. The thickness of the floor of the hind-brain in the median line is shown in fig. 24 G, *w. H. B.*

Before the embryo of Amblystoma has reached the stage of development represented by fig. 17 G, the first development of nerve-fibres has taken place in the central nervous system. The arrangement of these nerve-fibres corresponds very closely to the first arrangement of the nerve-fibres in the Lizard, and the arrangement seems to be identically the same in Triton and Rana. The nerve-fibres in the neural tube of the dorsal region first appear as two flat bands of longitudinal fibres, lying next the lateral surfaces of the tube. Fig. 34 shows a section of the neural tube of Amblystoma in the anterior dorsal region. The band of longitudinal fibres (*L. F.*) extends nearer to the ventral median than to the dorsal median surface of the tube. Goette has described these fibres as originating in the external halves of the peripheral cells throughout this portion of the tube; while the internal half of each cell, with the nucleus, becomes one of the cells of the grey matter. These points I have not been able to follow out with the material at my command. Shortly after the longitudinal fibres have appeared another system of fibres arises—the transverse fibres or ventral commissure (*T. F.*). These fibres appear as polar outgrowths of the cells which lie internal to the longitudinal band. They pass ventrally along the inner surface of the longitudinal band, and cross transversely the ventral surface of the neural tube immediately inside the cuticula. Both of these systems of nerve-fibres develope later in the posterior than in the anterior part of the central nervous system. The transverse fibres extend as a continuous ventral commissure as far forward as the point where the floor of the mid-brain bends ventralwards into the posterior wall of the infundibulum. This is shown in median vertical section in fig. 24 G. The lateral bands of longitudinal fibres extend forward through the hind- and mid-brain, showing the same relations as in the dorsal region (fig. 34). On passing from the mid-brain to the fore-brain the lateral bands follow the curve of the cranial flexure; and on reaching the morphologically anterior surface of the brain, they cross it, blending with each other immediately ventral to the optic stalks. The lateral bands thus blend into an anterior band, which is cut transversely into the median vertical sections, 17 G and 18, at *Ch.* This anterior band comprises a bundle of fibres, which I would roughly estimate to be about twenty times as large as the bundle of fibres which appears shortly afterwards on each optic stalk. The course of the lateral band (*L. F.*) in the mid- and fore-brain is shown in the lateral vertical section fig. 32 G; the dotted line indicates the lower median contour of the brain. Fig. 33 shows the anterior band (*A. F.*) of the Frog just behind the optic stalks. This section is cut transverse to the long axis of the embryo. No fibres appear in the region of the infundibulum which lies between the anterior band and the anterior edge of the above-described continuous ventral commissure. Of the brain commissures (not including the anterior band) the posterior commissure is the first to appear. It developes about the time that the ventral commissural system appears. The posterior commissure is shown at *P. C.*, figs. 18, 32 G, and 35. It crosses the dorsal surface of the brain immediately posterior to the epiphysis. Its fibres seem to be not continuous with the fibres of the lateral bands, but, as far as they can be traced, they cross the course of the lateral bands; losing themselves, however, in the region of the latter. The anterior commissure developes relatively much earlier in Amblystoma than in the Lizard. It first arises as two lateral symmetrical bundles of fibres, passing along the exterior surfaces of the corpora striata and intersecting the lateral bands just posterior to the optic stalks (*A. C.*, fig. 32 G). This section shows that these fibres are not continuous with the fibres of the lateral bands. A part of these bundles of fibres crosses the anterior surface of the brain a short distance dorsal to the optic groove at the point *A. C.* in figs. 18 and 30 H. The rest of these fibres continue on toward the roots of the olfactory nerves, *n. I*, fig. 29 H. A short time after the anterior band has appeared, there appears on the morphologically anterior surface of each optic stalk a small growth of nerve-fibres, developing as far as can be seen, in exactly the same manner as the development of the fibres of the lateral longitudinal bands. These optic fibres appear at the point *n. II*, in fig. 32 G (Amblystoma), and are shown in fig. 33 (Frog), where they are cut nearly longitudinally. The latter section shows that no fibres appear in the posterior wall of the optic stalk (*op.*). Medianly, the optic fibres meet and blend with the anterior band; distally, they pass unbroken into the inner surface of the eye-cup (fig. 33). I have not followed the later growth of the optic nerve in the Amphibia, but I judge from the close similarity between this stage and a stage in the Lizard, that the development of the optic nerve in the Amphibia is throughout about the same as I have described it for the Lizard.[1]

Figs. 27 H—30 H show four horizontal sections through the head of an embryo of Amblystoma at an age corresponding to that of fig. 18. These sections show the nerve-fibres of the brain at a more advanced period than that above described. Of these sections, 27 H is cut nearest the dorsal surface of the head, and on the left side passes above the lateral band of longitudinal fibres (*L. F.*) in the region of the secondary cranial flexure just in front of the ear. On the same side of the section the lateral band in the hind-brain is seen to be continuous with the lateral band in the mid-brain (*L′. F.*). In front of the mid-brain is seen the posterior part of the cerebral hemispheres. The next more ventral section (28 H) passes through the thalamencephalon and through the fold which separates the infundibulum (*In.*) from the hind-brain. In the hind-brain may be seen the transverse fibres of the ventral commissure (*T. F.*). These are also visible (*T. F.*) in section 29 H, the hind-brain in this section being cut tangentially to its ventral convexity. In this same section may be seen on the right hand side the connection between the lateral band and those fibres which run dorsally along the corpora striata. One part of these fibres forms the anterior commissure as above mentioned (fig. 30 H, *A. C.*); while the other part continues onward to the region of the olfactory nerve (*n. I*), and here blends with a superficial layer of nerve-fibres, which covers the lateral dorsal part of each hemisphere, and extends so far upwards and backwards as to appear in section 27 H. Fig. 30 H shows the brain in section very near its anterior surface. At *A. F.* may be seen the fibres of the anterior band, with the fibres of the optic nerve (*n. II*) blending with its dorsal edge. At *A. C.* may be seen the fibres of the anterior commissure. Between the thickening of the anterior band and the anterior commissure appears the optic groove (*o. g.*).

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[1] Orr, "Contribution to the Embryology of the Lizard," 'Journal of Morphology,' vol. i, No. 2, 1887.

Orientation as to the direction of this section through the brain may be easily acquired by comparing it with fig. 18. The section 30 H would be perfectly horizontal in the fig. 18. Thus it enters the brain at the hinder edge of the anterior band and passes forward at an acute angle to the morphologically anterior surface of the brain. In this way the fibres passing from the region of the lateral bands to the anterior commissure are cut obliquely. The relations of these fibres to the lateral bands are shown in fig. 32 G. Here it appears that they do not bend and run with the lateral bands, but may be traced for some distance, crossing the latter at right angles. The anterior commissure is at first undivided and lies next to the surface of the brain, but in the latest stage which I have examined an internal part has become divided off from the superficial part (fig. 18). This internal part I judge to be the corpus callosum.

The growth of the hind-brain, together with its change of form, has in this oldest stage brought the cranial nerves of this region much nearer together. These conditions are illustrated in figs. 27 H and 28 H. The nerve-roots which are present form very large ganglia. The common ganglion of the seventh and eighth nerves (*n. VIII, VII*) lies relatively much nearer the root of the fifth nerve (*n. V*) than it did at the time of its first appearance. The roots of the ninth and tenth nerves appear to have fused in a common ganglion (*n. X, IX*). This may be due to the great growth of the auditory vesicle pushing the root of the ninth nerve backward. I have been unable to find in these stages any traces of the third, fourth, and sixth nerves. In the Lizard the third nerve developes as soon as the other ventral roots of the nervous system; the sixth nerve developes somewhat later than the other cranial nerves, except the fourth, which first appears at a stage much later than the present stage of Amblystoma. The olfactory nerve (*n. I*) is shown in fig. 29 H, entering the olfactory sac (*N. a.*). The course of this nerve from its origin in the fore-brain is backwards and downwards. The fibres of the optic nerve are also shown in fig. 30 H, entering the brain at *n. II,* where they join the forward or dorsal edge of the anterior band of fibres (*A. F.*).

Appendages and Skeleton of the Head.

The gill-clefts develope in Amblystoma after the usual manner from before backward. The first or hyoid cleft (*I*) does not break through, but forms like the others a laterally extended hypoblastic pouch (figs. 15 F, and 26). In the case of the hyoid this pouch extends in a ventral and median direction, forming a groove which meets a similar groove from the opposite side. The median portion of this groove is shown in the longitudinal vertical section of fig. 18, *Th.* From comparisons with the work of other writers I suppose this part marked *Th.* to be the rudiment of the thyroid gland, though in this case I have traced the development no farther. Whether this relation of the thyroid rudiment to the hyoid clefts can be considered as an argument for the phylogenetic origin of the thyroid gland from the ventral coalition of the hyoid clefts, is, I think, doubtful. The ventral groove may be the result of the early development of the tongue-rudiment. In the Lizard the hyoid clefts are widely open to the outside, and the thyroid rudiment appears between the transverse areas of the hyoid and first branchial clefts. The thyroid rudiment in the Lizard has no apparent connection with the hyoid clefts.

In the stage represented in fig. 15 F, the hyoid (*I*) and the first two branchial cleft-rudiments (*II, III*) have appeared; in the stage of fig. 26 five in all have appeared (*I—V*), but none of them have as yet broken through. These stages show the development of the head-cavities or mesoblastic somites of the head. The anterior somite is the first to develope, and appears just behind the eye. The other somites are separated off from this first one by the successive development of the hyoid and branchial clefts. These somites of the head do not attain a characteristic development as cavities as is the case with Elasmobranchs and the Lizard. Nevertheless there is here a tendency in that direction, and sometimes a slight cavity appears as in fig. 26, *H.C.* Where this happens it is generally in the most anterior somites.

Previous to the breaking open of the gill-clefts there appears on each side of the mandibular arch a small thickening and protrusion of the epiblast. These protuberances appear long before any of the external gills of the other arches. They become later rod-like structures, and are then easily recognised as the organs which Clarke has called "balancers." An examination of their structure and relations shows them to be homologous with the external gills. They are supplied with blood by the most anterior or mandibular fork of the ventral aorta, and a branch of the fifth nerve may be traced down to the neighbourhood of the base of each balancer. Fig. 25 shows a vertical section passing longitudinal to the axis of the embryo and nearly longitudinal to the balancer (*bl.*). The balancer consists of a cylinder of compact epiblastic tissue, growing slightly thicker toward the distal end, where it forms a thick epiblastic cap similar to the epiblastic cap generally observed on the limb-rudiments of vertebrate embryos. Internally the balancer is nearly hollow, but is generally divided longitudinally through the greater part of its proximal length by a thin membranous network of which the function is probably to separate the courses of the arterial and venous blood. The large amount of blood which passes through the balancer indicates that it subserves in part a respiratory function. Balfour, following the account of Goette, has stated that the mandibular artery is never developed in Amphibians. In Amblystoma I find the mandibular artery developed, though in a less degree than the posterior branchial arteries. Owing to the early disappearance of the balancers this artery probably atrophies at an early date. Though my sections of Triton were not so favorable to the observation of this point, yet I find traces there of the existence of a mandibular artery.

At a stage when the branchial clefts have broken through and the cartilaginous skeleton has appeared (fig. 30 H), the relation of the balancer to the mandible becomes even more pronounced. The quadrate cartilage sends out laterally a crescent-shaped process immediately above the articulation with the Meckelian cartilage. This process extends to the base of the balancer separating the two blood-vessels which pass to and from the balancer. This process appears crescent-shaped only in vertical longitudinal section, and the posterior blood-vessel lies partly enclosed in the crescent. The process is shown at *p.* in the horizontal section, fig. 30H. Here also may be seen a bundle of muscle-cells extending from the pterygoid muscle (*m.*) into the base of the balancer (*bl.*). Another band of apparently undifferentiated muscular elements passes from the end of the above-mentioned process down into the balancer. Section 30H is cut through the base of the balancer, the free end of which extends below the plane of the section.

The balancers of Triton are of the same character as those of Amblystoma, but in Triton they appear to be not quite so highly developed.

Clarke observed the use of the balancers in the living embryos, and came to the conclusion that the chief function of the organs was as a means of support for the embryos to prevent them from sinking into the slime on the bottom of the pools in which they live. My own observations on the living embryos have led me to the same conclusion. It seems therefore that we have in this case not only the peculiarity of a homologue of the external gills arising from the mandibular arch, but also a homologue of the external gills becoming metamorphosed into an organ for the support of the body. It is also noteworthy that the balancers drop off after the limbs have appeared.

If we seek among the Anura for organs homologous with these balancers of the Urodela, the only organs which we can fix upon with any degree of probability are the suckers of the tadpole. Balfour has stated that these suckers arise on the hyoid arch, but in the embryos of Anura which I have examined they appear immediately posterior to the mouth-fusion (fig. 20) long before any trace of a division into visceral arches has appeared. I think for this reason that the suckers cannot properly be assigned to the hyoid arch. Balfour, in describing the embryology of the Urodela ('Comp. Embry.'), says, "Stalked suckers of the same nature as the suckers of Anura are formed on the ventral surface behind the mouth." The balancers in the two forms of Urodela which I have examined possess none of the characteristics of suctorial organs. Yet the balancers of the Urodela and the suckers of the Anura serve ultimately the same purpose, namely, to prevent the embryos from sinking into the soft organic mud usually found in the bottom of the pools which they inhabit, immersion in which would undoubtedly prove fatal to large numbers. An examination of a larger number of species may bring to light intermediate forms of these organs which would prove a more direct homology between the balancers and suckers.

The condition of the branchial apparatus and the skeleton of the head at a time when the branchial clefts have opened and shortly after the cartilage has appeared, is shown in figs. 27 H—31, and also fig. 18. Fig. 31 is an approximate reconstruction from drawings of sections in three planes at right angles to each other; it represents the skeleton of the left side of the head. The four branchial clefts (*II—V*) are situated between the hyoid arch (*I′*) and the posterior branchial arch (*V′*, fig. 30 H). Each of the posterior four cartilaginous arches (*II′—V′*, fig. 28 H) supports an external gill. The cartilaginous hyoid arch has no external gill, but supports an opercular fold (*o. f.*, fig. 30 H) which extends transversely across the ventral side of the head (fig. 18, *o. f.*) and a short distance up the lateral sides, partly overlapping the external gills. The cartilaginous bars of the visceral skeleton are of unequal length. Only the hyoid and the first two branchial bars extend to the median line, where they unite in a basi-hyobranchial plate of cartilage (*B. Hy.*, figs. 31 and 18). From this basi-hyobranchial plate there extends in a ventral and posterior direction a long curved process of which the flattened end touches the pericardium. The posterior two branchial bars (*IV′*, *V′*) each unite with the next preceding bar as shown in fig. 31. The hyoid bar does not extend dorsalwards more than half as far as the first branchial bar, so that in the sections of series H it first appears in the section 30 H. Each of these five bars is supported dorsally by a small muscle; the muscles are shown at *m'*. *m'*. in fig. 27 H. Dorsally the four branchial bars are united by a continuous piece of cartilage, *c. b.*, fig. 27 H. None of these bars are articulated into different pieces, but the hyoid and first two branchial bars show ventrally a rudimentary beginning of an articulation.

The cranial skeleton of Amblystoma at this stage shows certain peculiarities, the homologies of which I am unable to determine in other forms. A general idea of the shape of the skeleton may be derived from fig. 31 and series H. Each lateral half of the cranial skeleton, together with the corresponding quadrate, appears as one continuous piece of cartilage. Of this piece the parts corresponding to the trabecular (*tbr.*) and parachordal (*prc.*) cartilages are easily distinguished; the former lying along the anterior surface of the brain, and the latter lying along the floor of the hind-brain adjacent to the notochord. The trabeculæ do not meet anteriorly. From the anterior end of the parachordal region there extends in a dorso-lateral direction a small bar of cartilage (*x*, figs. 31 and 28 H). This is met by another bar of cartilage (*y*), which extends upward and backward from the trabecula at the region of the optic nerve. These two bars (*x* and *y*) form thus a triangle, of which the base is the posterior part of the trabecula. At the junction of the anterior bar (*y*) with the trabecula there is a foramen through which passes the optic nerve (*n. II*, fig. 31). The greater part of the bar marked *y*. appears to pass dorsal to the optic nerve (fig. 31). This bar is a relatively thin piece, and separates the eyeball from the thalamencephalon. The posterior bar (*x*) of the triangle lies in the lateral groove between the floor of the hind-brain and the infundibulum, that is, lateral to the fold caused by the primary cranial flexure. At the dorsal apex of this cartilaginous triangle the cartilage is continuous with the dorsal proximal part of the quadrate cartilages (*Q.*). This is seen at *Q. x, y*, in figs. 27 H and 28 H. The dorsal part of the quadrate cartilage is rather thin, and lies transversely with its lateral edge curved posteriorly toward the otic cartilage; farther ventralwards its section is shown in figs. 29 H and 30 H. The Meckelian cartilage shows no unusual peculiarities. Anteriorly it is connected with the cartilage of the opposite side by a short band of undifferentiated connective tissue.

What the significance of this manner of development of the chondrocranium may be, or how much importance should be attached to it, I am unable to say, as I have observed it only at this one stage.

At this stage well-characterised rudiments of teeth have appeared (*d.*, figs. 30 H and 18). They are present in a semicircle above the Meckelian cartilages. They do not appear in a single row, but in several irregular rows. In the same manner they appear just ventral to the trabeculæ cranii along those parts of the trabeculæ which lie anterior to the optic nerve. In a cross section of the several irregular rows of teeth the teeth seem to radiate from the bar of cartilage on which they rest. In this respect the trabeculæ cranii and the Meckelian cartilages present the same appearance.

GENERAL CONCLUSIONS.

The central nervous system of Amphibians first appears as a transverse epiblastic thickening dorsal to the mouth-fusion, and continuous with paired elongated epiblastic thickenings lying dorsally on each side of the median line.

The primary cranial flexure is due to the presence of the transverse epiblastic thickening (anterior medullary plate).

The transverse epiblastic thickening forms, when the brain is enclosed, that part of the brain wall which lies between the infundibulum and the optic groove (i. e. the depression just dorsal to the chiasma of the optic nerves).

The first nerve-fibres which develope in the brain appear on what was originally the internal surface of the primitive epiblastic thickenings running longitudinally in the dorsal region and uniting continuously in the region of the primitive transverse thickening.

A subsequent development of nerve-fibres gives rise to a continuous ventral commissure extending through the floor of the mid-brain and hind-brain and spinal cord; and to the anterior and posterior commissures of the brain.

The fibres of the optic nerves are intimately connected with and are developed in the same manner as the main bundle of fibres in the region of the primitive transverse epiblastic thickening.

The hypophysis of Amblystoma presents a form of development intermediate to that of the Lizard and that of the Frog.

The balancers of Amblystoma may be considered as external gills of the mandibular arch which have become metamorphosed into embryonic organs of support.

P.S.—In his work entitled 'Untersuchungen über die vergleichende Anatomie des Gehirns,' Dr. Ludwig Edinger has described a Commissur der basalen Vorderhirnbündel, which he says appears in all classes of Vertebrates. The position of this Commissur in the adult brain immediately behind the optic chiasma is identical with that of the anterior band of nerve-fibres (*A. F.*), which I have described in the embryonic condition. The relatively large size and pronounced character of the anterior band in both Reptilian and Amphibian embryos lead me to think that it was once of primary importance, and that the Commissur in the adult brain is probably a rudiment of the same with changed relations and functions.

EXPLANATION OF PLATES XXVII, XXVIII, & XXIX,

Illustrating Mr. Henry Orr's paper "Note on the Development of Amphibians, chiefly concerning the Central Nervous System; with Additional Observations on the Hypophysis, Mouth, and the Appendages and Skeleton of the Head."

Where a number of figures represent sections of the same individual embryo, all those figures have the same letter affixed to their numbers.

All figures of sections have been drawn with the Abbey camera lucida and a Zeiss's microscope, so that in figures magnified to the same degree the size of the parts may be directly compared. (Z. 2, A, means Zeiss's ocular 2, and objective A, &c.)

Index Letters.

A. C. Anterior commissure of fore-brain. *A. F.* Anterior medullary fold. *A. F′.* Anterior band of nerve-fibres, continuous with the lateral bands, *L. F.* *a. M. P.* Anterior medullary plate. *B. Hy.* Basi-hyobranchial plate of cartilage. *Bl.* Region of the blastopore. *bl.* Balancers. *c. b.* Cartilaginous bar connecting dorsally the cartilaginous gill-arches. *Ch.* Optic chiasma united with the anterior band of nerve-fibres (*A. F′.*). *d.* Dental rudiments. *E.* Ear. *Ep.* Epiblast. *Eph.* Epiphysis cerebri. *Ey.* Eye. *F. B.* Fore-brain. *G—g.* See explanation of Figs. 2 A—5 D. *H. B.* Hind-brain. *H. C.* Head cavity. *Hph.* Hypophysis. *Ht.* Heart. *Hyp.* Hypoblast. *In.* Infundibulum. *L.* Lens of eye. *L. F.* Primary longitudinal fibres of central nervous system; *L. F′.* the same in the region of the thalamencephalon. *M.* Mouth-fusion or mouth. *m.* and *m′.* Pterygoid and branchial muscles. *M. B.* Mid-brain. *Md.* Medulla spinalis. *Mes.* Mesoblast. *M. F.* Lateral medullary fold. *mk.* Meckelian cartilage. *M. P.* Lateral medullary plate. *N.* Notochord or rudiment of the same. *Na.* Nasal sac. *n. I, n. II—n. X.* Olfactory, optic, and succeeding cranial nerves. *o. f.* Opercular fold of the hyoid arch. *o. g.* Optic groove. *o. p″.* Posterior wall of the optic stalk. *p.* Lateral cartilaginous process of the quadrate at the base of the balancer. *P. C.* Posterior commissure of the brain. *p. g.* Rudiment of the pectoral girdle. *Ph.* Pharyngeal cavity. *So.* Somatopleure of mesoblast. *Sp.* Splanchnopleure of mesoblast. *St.* Corpora striata. *tbr.* Trabeculæ cranii. *T. F.* Transverse nerve-fibres forming a continuous ventral commissure. *Th.* Rudiment of the thyroid gland. *w. H. B.* Floor of hind-brain. *x—y.* See explanation in text, p. 319. *Y.* Yolk. *I—V.* Hyoid and branchial clefts. *I′—V′.* Cartilaginous gill-arches.

PLATE XXVII.

FIG. 1.—Median-longitudinal and nearly vertical section of the egg of Amblystoma, at a time when the medullary plates have first appeared. It shows the anterior epiblastic thickening (*a. M. P.*), which unites anteriorly the two dorsal medullary plates. Also the thinner median portion (*g. g.*) between the dorsal medullary plates. *Bl.* Region of the blastopore. *N.* Undifferentiated hypoblastic tissue of the notochord. (Z. 2, A A.)

FIGS. 2 A, 3 B, 4 C, and 5 D.—Transverse sections through the anterior dorsal region of embryos of Amblystoma, showing successive stages of development. The first of the series (2 A) is at a stage corresponding with that of Fig. 1. *G.* The thinner median portion of epiblast between the dorsal medullary plates which becomes pushed downwards, so that the surfaces immediately lateral to it become pressed together along the line *g.* (Z. 2, A A.)

FIGS. 6 A, 7 B, 8 C, 9 D.—Transverse sections through the anterior region of the head of the same embryos respectively as Figs. 2 A—5 D. These sections show the anterior medullary plate (*a. M. P.* or *A. F.*) which connects the lateral dorsal medullary plates. *A. L.* Anterior end of the alimentary cavity. (Z. 2, A A.)

FIG. 10 D.—Transverse section through the posterior region of the head to show the reduction of the lumen of the neural canal. (Z. 2, A A.)

FIG. 11.—Transverse section through the cervical region of an embryo of Amblystoma, somewhat more advanced than that of series D, showing the change of shape in the neural tube and canal. (Z. 2, A A.)

PLATE XXVIII.

FIGS. 12 E and 13 E.—Longitudinal and nearly vertical sections of an embryo of Amblystoma (at a stage represented by Clarke's Fig. 14). Fig. 12 E passes through the vertical plane at the hypophysis (*Hph.*) and the dorsal notochord; Fig. 13 E at the anterior end of the notochord and the epiphysis (*eph.*). (Z. 2, A A.)

FIGS. 14 F, 15 F, and 16 F.—Horizontal sections of an embryo of Amblystoma at the same stage as the preceding two figures. Fig. 14 F passes through the hind-brain and part of the dorsal medulla. Fig. 15 F passes through the mid-brain and the dorsal part of the alimentary cavity. Fig. 16 F passes through the hypophysis and the anterior part of the fore-brain. (Z. 2, A A.)

FIGS. 17 G and 18.—Longitudinal median vertical sections of two embryos of Amblystoma. 17 G is older than the stage of series E and F, and 18 is older than 17 G. These sections, together with 12 E, show the development of the lower jaw, the formation of the mouth, and the hypophysis. (Z. 2, A A.)

FIGS. 19—23 inc.—Longitudinal median vertical sections of successive stages of Frog-embryos, showing the formation of the fore-brain, the hypophysis, and the mouth-fusion, with their relative changes of position. (Z. 2, A A.)

Fig. 24 g.—Part of a longitudinal median vertical section of an embryo of Amblystoma, showing the floor of the hind-brain and the fold between the hind-brain and infundibulum, which is caused by the primary cranial flexure. (Z. 2, A.)

Fig. 25.—Taken from a series of longitudinal vertical sections of an embryo of Amblystoma; it shows the balancer in nearly longitudinal section, and also a superficial portion of the mandibular arch. (Z. 2, A.)

PLATE XXIX.

Fig. 26.—Horizontal section of an embryo of Amblystoma at a stage between the stages e—f and the stage g. This figure shows the first formation of the optic lens, also the formation of the gill-clefts and the somites of the head. (Z. 2, A A.)

Figs. 27 h—30 h incl.—Horizontal sections of an embryo of Amblystoma at the same stage as the embryo of Fig. 18. Of these sections, 27 h is the most dorsal and 30 h the most ventral, the others being intermediate in the order of their numbers. The sections show the development of the nerve-fibres in the brain, and the early development of the cartilaginous skeleton and the branchial apparatus. (Z. 2, A A.)

Fig. 31.—Approximate reconstruction of an early stage of the cranial and visceral skeleton of Amblystoma, made from drawings of series of sections cut in three planes at right angles to each other. It shows the skeleton of the head viewed from the left side, also the shape and relative position of the left rudiment of the pectoral girdle (*P. g.*).

Fig. 32 g.—Lateral longitudinal vertical section of the brain of an embryo of Amblystoma, cut through the left side, showing the course of the nerve-fibres at the time of their first development in the brain. (Z. 2, A.)

Fig. 33.—Part of a transverse section through the fore-brain of a Frog-embryo, showing the fibres of the lateral and anterior band (*L. F.* and *A. F.*), the latter crossing the anterior surface of the brain; also the fibres developing on the anterior wall of the optic stalk (*n. II*). The posterior wall of the optic stalk (*o. p''.*) is free from fibres. (Z. 4, A.)

Fig. 34.—Transverse section of the spinal cord in the dorsal region of an embryo of Amblystoma at the stage of series h. It shows in cross-section the longitudinal nerve-fibres of the lateral band (*L. F.*), also the transverse fibres of the ventral commissure (*T. F.*). (Z. 4, A.)

Fig. 35.—Transverse section passing through the mid-brain and secondary fore-brain of an embryo of Amblystoma at the same stage as the embryo of series g. It shows the corpora striata (*st.*) and the transverse fold which separates the secondary fore-brain from the thalamencephalon. *P. C.* shows the position of the posterior commissure. (Z. 2, A A.)

Fig. 1.

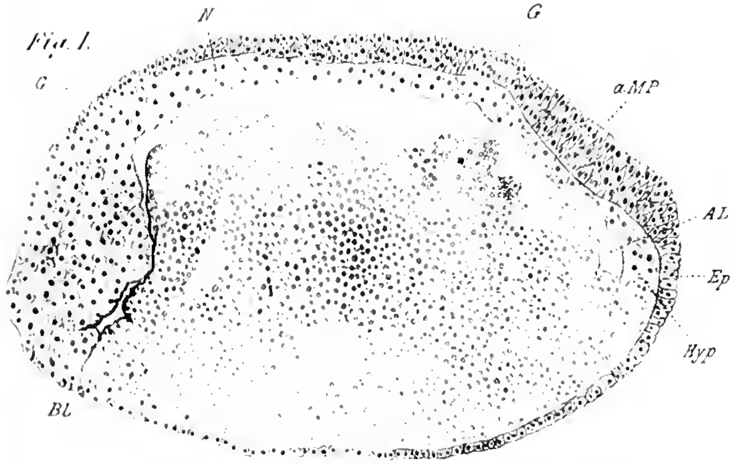


Fig. 4. C.

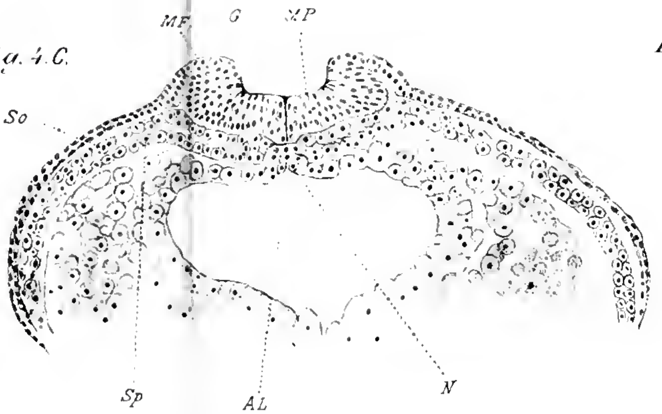


Fig. 8. C.

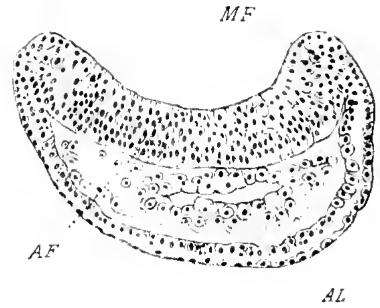


Fig. 5. D.

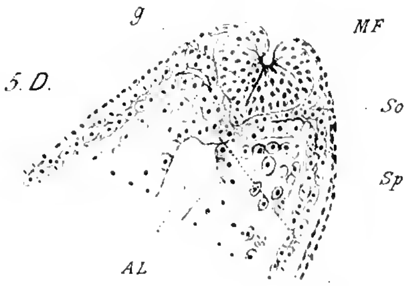


Fig. 2. A.

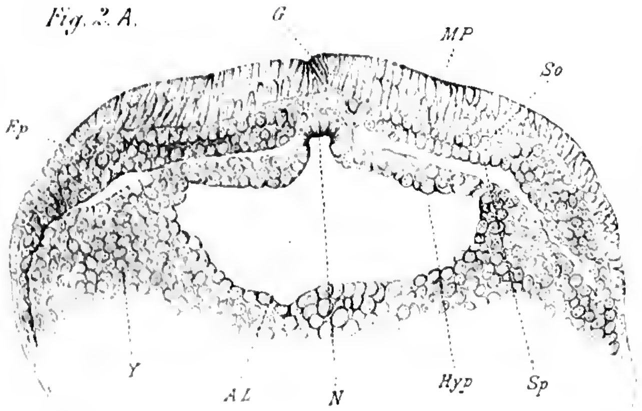


Fig. 6. A

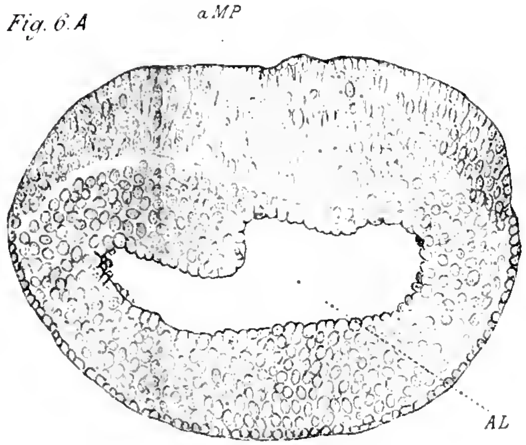


Fig. 10. D.

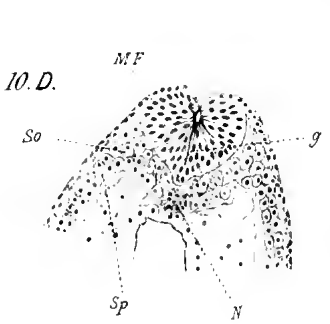
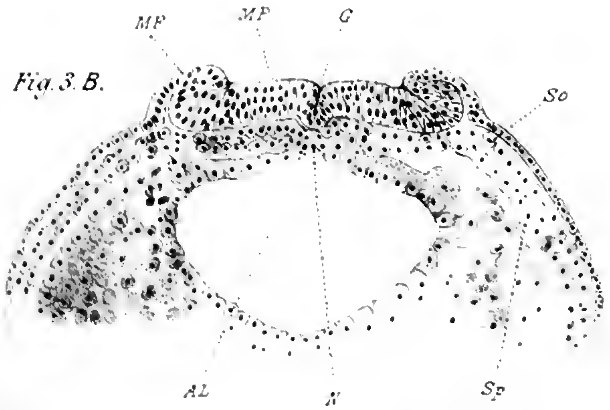


Fig. 3. B.



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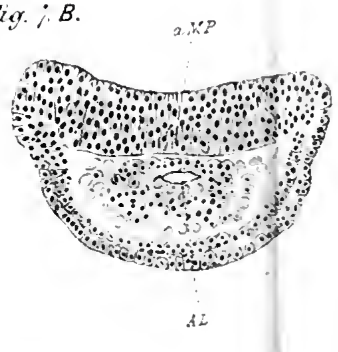


Fig. 11.

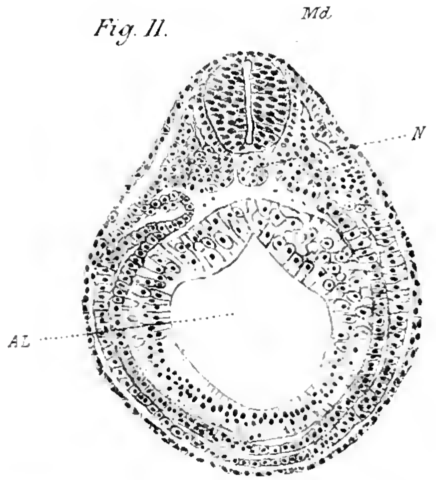
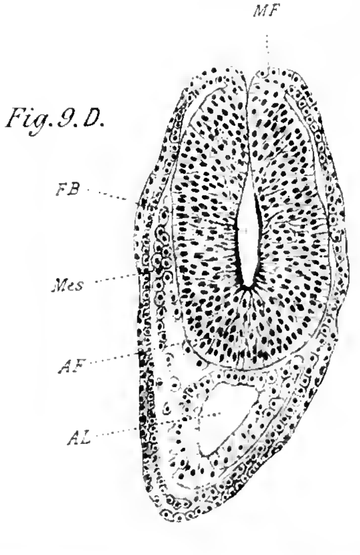


Fig. 9. D.



Orr del.

F. Huth, Lith^r Edin^r

Fig. 12. E.

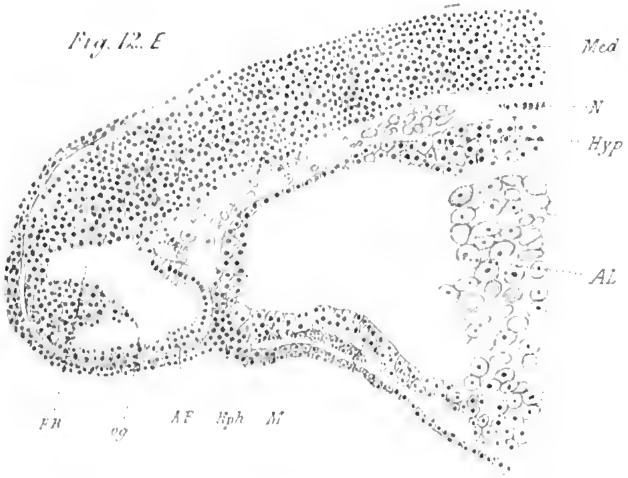


Fig. 14. F.

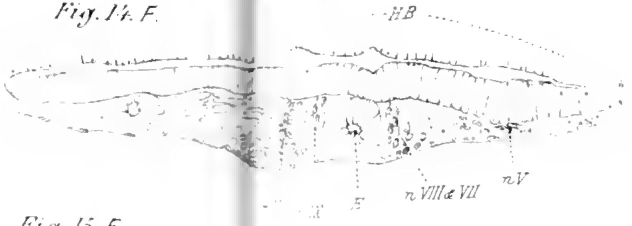


Fig. 15. F.

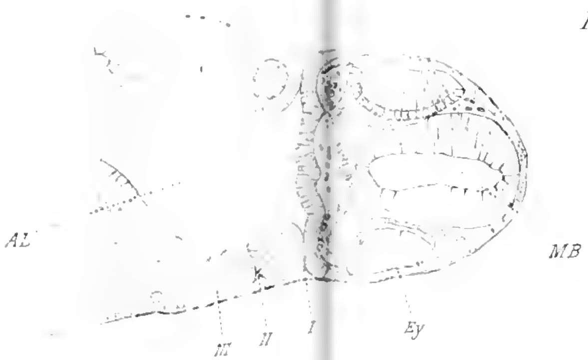


Fig. 13. E.

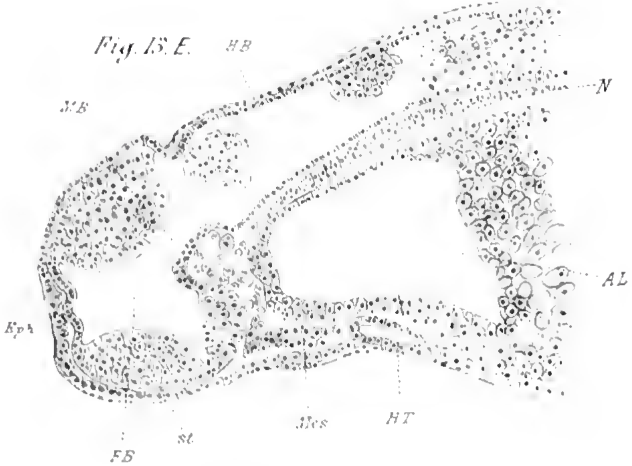


Fig. 16. F.

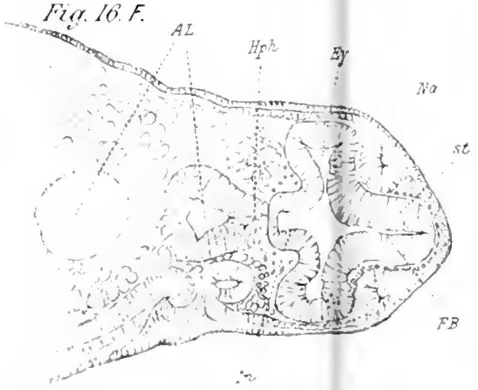


Fig. 17. G.

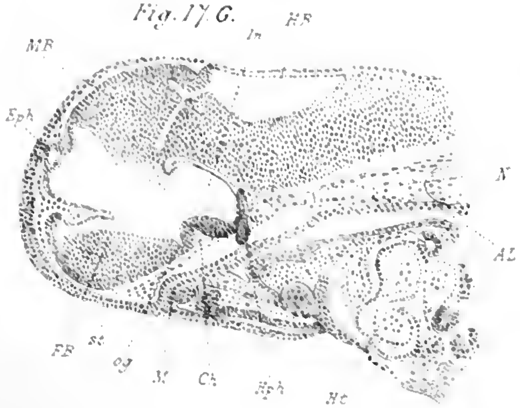


Fig. 18.

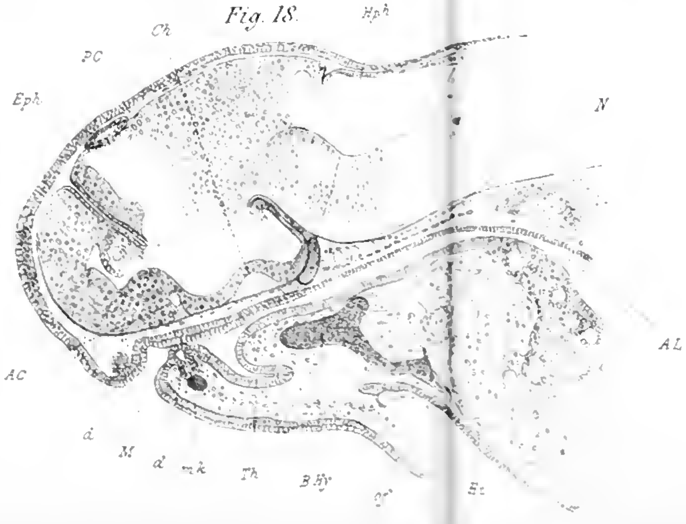


Fig. 19.

Fig. 20.

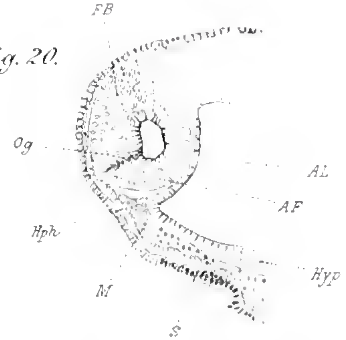


Fig. 21.

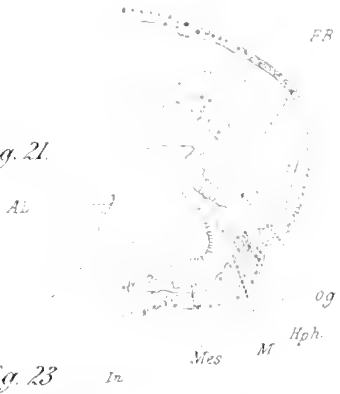


Fig. 22.

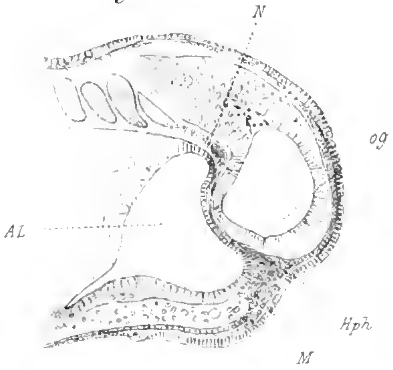


Fig. 23.

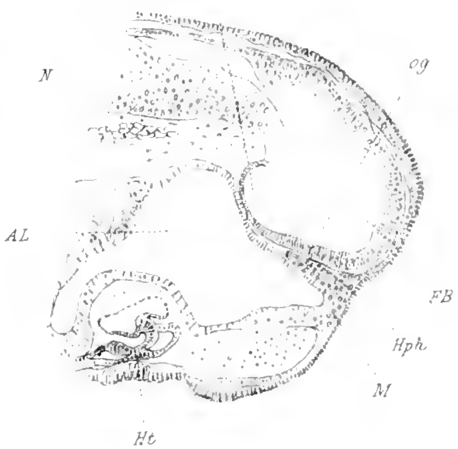


Fig. 24. G.

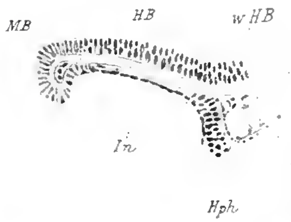


Fig. 25.

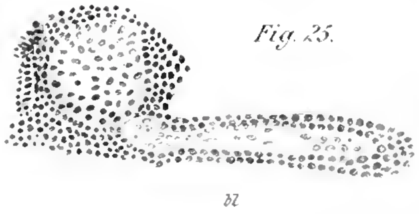


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Fig. 26.

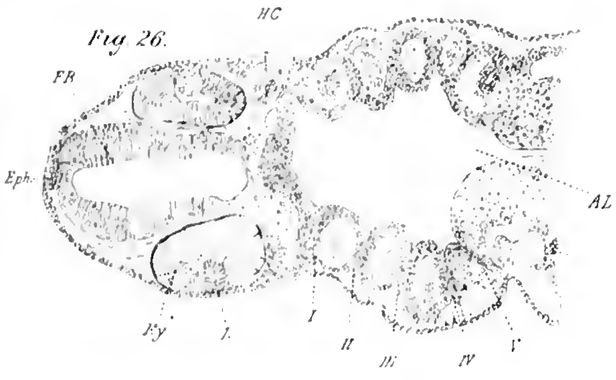


Fig. 29. H.

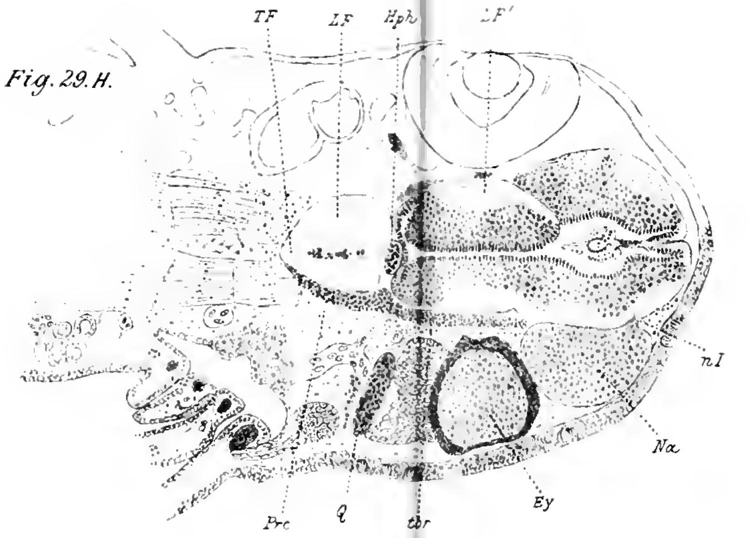


Fig. 32. G.

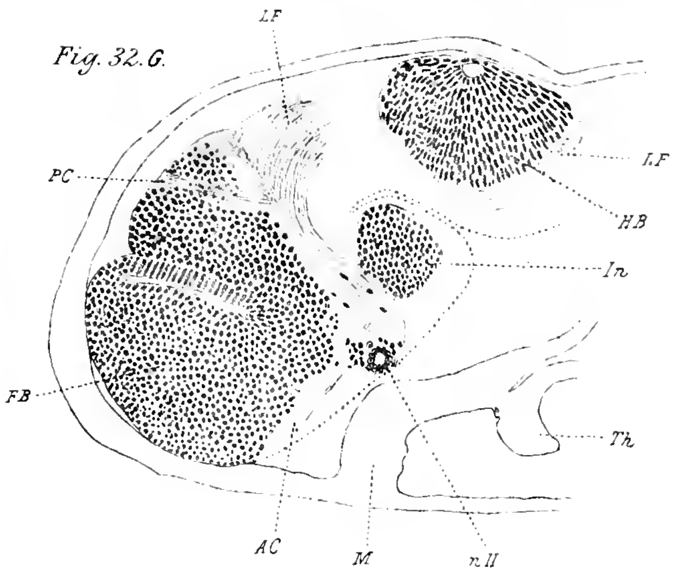


Fig. 27. H.

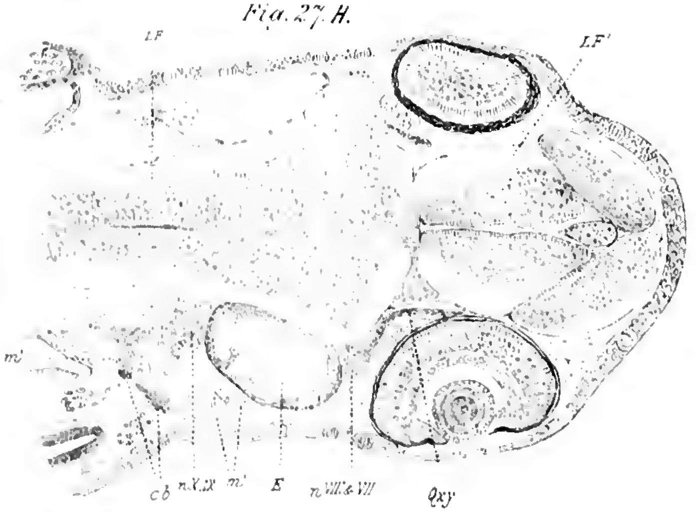


Fig. 30. H.

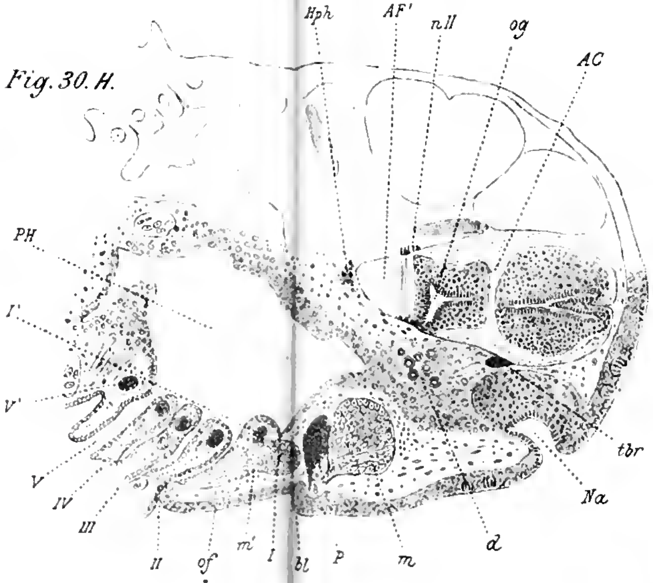


Fig. 33.

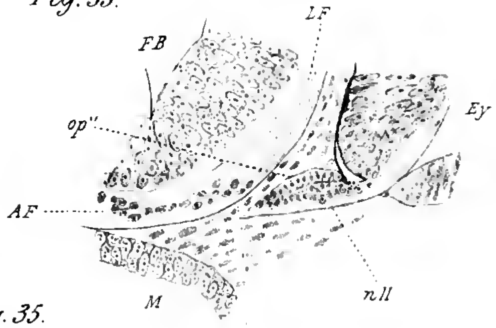


Fig. 35.

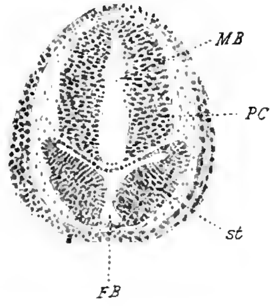


Fig. 28. H.

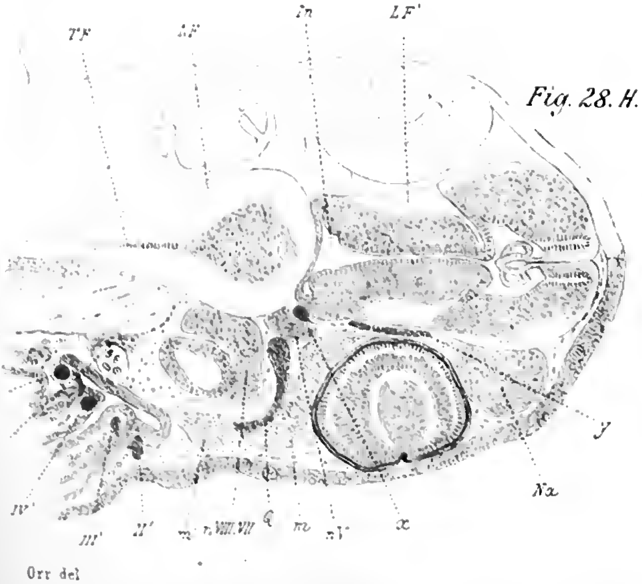


Fig. 31.

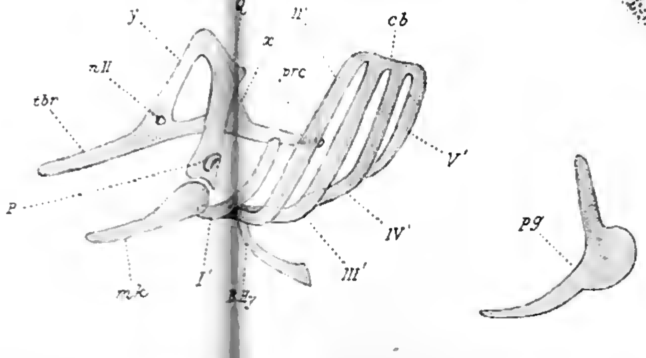
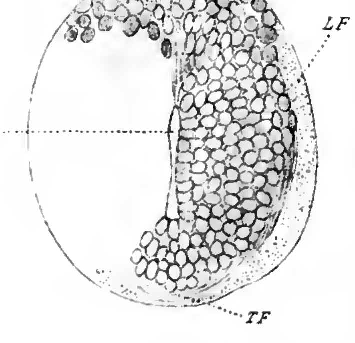


Fig. 34.



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Studies on the Comparative Anatomy of Sponges.

II. On the Anatomy and Histology of Stelospongus flabelliformis, Carter; with Notes on the Development.

By

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Demonstrator and Assistant Lecturer in Biology in the University of Melbourne.

With Plates XXX, XXXI, XXXII, & XXXIII.

The species upon the study of which the present paper is based, was first described by Mr. H. J. Carter, F.R.S., in 1885 (6), under the name Stelospongus flabelliformis. The first specimens were dredged by Mr. J. Bracebridge Wilson, M.A., and forwarded by him to England as part of a large collection entrusted to Mr. Carter for description. Mr. Carter's description is unfortunately brief and unaccompanied by figures, and he does not enter into any details concerning the anatomy of the Sponge. He notes, however, in a subsequent paper (7), that it is characterised by the presence of very large embryos, and this remark first led me to the identification of my specimens.

During the last Easter vacation it was my good fortune to spend some days in dredging with Mr. Bracebridge Wilson in the neighbourhood of Port Philip Heads, and amongst numerous other interesting Sponges we happened to obtain a horny Sponge which, when torn open, was found to contain a large number of enormous spherical embryos, each as large as a small pea, embedded in the choanosome. I picked out a number of these embryos from the living Sponge and placed them directly in strong spirit, and also preserved portions of the mother Sponge in the same way. This simple method of preservation, adopted at the time for want of other reagents, subsequently proved to have been highly successful.

After cutting sections of the embryos and finding that they presented certain very remarkable features, I determined to make a complete study of the anatomy of the adult Sponge. Fortunately, I found amongst a splendid collection of well-preserved Sponges already sent up to the Melbourne University by Mr. Wilson, several more specimens of Stelospongus flabelliformis, and I thus had abundance of material at my disposal.

My preparations were stained with borax carmine and cut in paraffin in the usual manner, and I found that in order to ensure success it was very important not to allow the temperature of the paraffin to rise above 128° F. Probably a lower temperature would have been better still, but unfortunately I had only hard paraffin to work with.

With regard to the figures, I may state that while some of them are more or less diagrammatic, all are taken from actual preparations, either individual or combined, with the exception of figs. 9 and 10, which are pure diagrams.

I have very great pleasure in taking this opportunity of expressing my sincere thanks to Mr. Bracebridge Wilson, to whom I am indebted for the whole of my material, and to Professor W. B. Spencer, who, throughout the progress of the work, has given me much valuable advice.

Anatomy and Histology.

External Characters.

An idea of the general appearance and size of the Sponge may be gained from fig. 1, which represents a fairly typical specimen, from which a portion has been cut off, drawn of the natural size. The Sponge consists of a stout cylindrical stalk terminating below in a basal expansion for attachment to the substratum, and above in a broad, compressed, but thick frond. Along the upper margin of the frond is a single row of large oscula.

The character of the surface of the frond is subject to considerable variations. On both sides it usually exhibits a number of prominent, branching, and anastomosing ridges, enclosing a number of concave depressions, as represented in the figure. The entire surface of the Sponge is more or less thickly encrusted with sand particles; these are, however, more abundant over the ridges than in the depressions. The latter are also characterised by a minutely reticulate appearance due to the presence in them of the inhalant pore-areas, each of which bears a number of pores. The pores are enormously abundant all over the depressed portions of the surface, but appear to be absent from the ridges.

The incrustation of sand already referred to gives to the surface of the Sponge a very hard, impenetrable character, and must form an admirable protection against the attacks of the numerous parasites to which Sponges are very subject. It functionally replaces the special dermal skeleton of spicules which exists in very many siliceous Sponges.

The Skeleton.

The skeleton (fig. 3) is composed of a rather irregular reticulation of cylindrical horny fibres, branching and anastomosing freely. The fibres are rather slender, and the meshes between them are wide, so that in thin sections the skeleton scarcely appears at all. As in most horny and siliceous sponges, it is easy to distinguish between two sets of fibres, primary and secondary. The primary fibres (fig. 3, *p. f.*) are long and rather stouter than the secondaries, measuring about 0·096 mm. in diameter. They radiate towards the surface of the Sponge, sometimes branching in their course, and end in the sandy incrustation. But they are most easily distinguished by the presence in them of numerous foreign bodies, grains of sand, broken sponge-spicules, &c., which form an axial core, surrounded and held together by concentric layers of spongin. The secondary fibres (fig. 3, *s. f.*) are short, and contain no foreign bodies. They run in various planes, and unite together adjacent primary fibres which they meet at various angles; they may also branch and anastomose inter se. They measure from about 0·048 to 0·08 mm. in diameter.

Thus the skeleton is thoroughly typical in structure and arrangement, and essentially the same as that of the ordinary bath-sponge, only much coarser. The distinction between the primary and secondary fibres is well marked. There is good reason to believe that primary fibres are phylogenetically of earlier origin than secondaries, and really very distinct from them. The primitive skeleton of the horny Sponges and of the siliceous (excluding the Hexactinellida) was probably composed simply of large, radiating spicules, or bands of spicules, coming out from a common centre, the centre of the Sponge. Such a condition occurs now very frequently amongst the Clavulina, Tethyadæ, and Tetractinellida, all of which groups we have reason to believe are more primitive than the Halichondrina and Ceratosa, which have reticulate skeletons. Amongst the Clavulina, Tethyadæ, and Tetractinellida there is usually little or no spongin present, but the spicules are very large, and arranged side by side in dense tufts radiating from a common centre. In the Halichondrina spongin is almost invariably present in considerable quantities, and the spicules gradually diminish in size as the amount of spongin increases, so that the fibres of the skeleton, instead of being stiff and rigid, become flexible and elastic. All stages in the gradual replacement of spicules by spongin may be traced in the large family of the Chalininæ, as I have endeavoured to show in a former paper (8). It is obvious that while a skeleton, composed solely of radiating primary fibres, would be very efficient so long as the fibres remained stiff and rigid, yet when the fibres became soft and flexible owing to the replacement of the spicules by spongin, such a skeleton would be almost useless. Hence arose the necessity for the formation of secondary fibres to connect the primaries together. A reticulate skeleton must therefore be regarded as derived from a radiate one by the development of secondary fibres connecting the primaries. There can no longer be any doubt that the majority, at any rate of the so-called "horny" Sponges, are descended, probably along several lines, from the Halichondrina, by the gradual loss of spicules and the greater development of spongin in a reticulate skeleton.

The occurrence of grains of sand in the skeleton fibres is not confined to the Ceratosa, for sometimes sand and spicules are simultaneously present in the fibres, as in Siphonochalina spiculosa (8). This replacement of spicules or of spongin by sand is no doubt of great advantage to the Sponge in saving material, and hence we not unfrequently get Sponges whose skeleton is entirely arenaceous (e. g. Dysidea).

In Stelospongus flabelliformis the skeleton fibres may sometimes be seen projecting freely from the surface of the Sponge (fig. 5, *f'*.), but this does not appear to be at all a constant character. It is difficult to understand how such a condition can have arisen; perhaps it is in some degree comparable to the projection of the spicules from the surface in very many siliceous Sponges.

In the stalk the skeleton is more strongly developed than elsewhere, and hence it acquires a tougher and denser character than the remainder of the Sponge.

THE CANAL SYSTEM.

(A) The Pores.

The inhalant apertures, or pores, are thickly scattered all over the depressed areas on the surface of the Sponge. Hence these areas might with some justice be termed pore-areas, in the sense defined by Ridley and Dendy in the Report on the "Challenger" Monaxonida (14). But there is an objection to the use of the term in this particular case in that these larger areas are themselves subdivided into a great number of smaller areas (fig. 4, *p. a.*), and as the latter are much better defined and more constant in size and relations than the former, it is better to apply the term pore-areas to them. These smaller areas appear to be strictly comparable to the pore-sieves of Phakellia ventilabrum, var. connexiva, or the pore-areas of Myxilla nobilis (14). Each one is an irregularly rounded or oval area, about 0·19 mm. in diameter, overlying a subdermal cavity, and each contains some five or six oval or rounded pores (fig. 4, *p.*) averaging about 0·05 mm. in their longer diameter.

The most satisfactory way of studying the arrangement and form of the pores in this and many other Sponges is to slice off as thin a portion as possible of the surface, and stain and mount in balsam in the usual way, without cutting sections. Fig. 4 represents such a preparation seen from above as a transparent object. The pores may also be seen in sections taken at right angles to the surface (fig. 2, *p.*), but in the present case it is rather difficult to obtain satisfactory sections of this kind owing to the presence of the sand grains in the ectosome.

(B) The Subdermal Cavities.

In this, as in my previous paper (9), I use the term subdermal cavities in the sense defined in the Report on the "Challenger" Monaxonida, i. e. to mean the spaces into which the pores directly lead. Sollas, in his article on Sponges in the 'Encyclopædia Britannica' (17), appears to make use of the term in a different sense, as synonymous with subcortical crypts, while he applies the term chones to the structures which I term subdermal cavities. The homologies of these various structures are not at present sufficiently understood to enable us to give them a really satisfactory nomenclature, and so I prefer to use a purely empirical one. The term subcortical crypt is used by Sollas and myself in the same sense, i. e. to mean the space underlying the cortex or ectosome into which the subdermal cavities (chones of Sollas) lead.

In Stelospongus flabelliformis each subdermal cavity (fig. 2, *s. c.*) is a hollow space corresponding in size and form to the pore-area which it underlies, and communicating with the exterior by means of the pores in its roof. The different subdermal cavities are separated from one another by anastomosing vertical walls of tissue constituting the bulk of the ectosome—represented as seen from above in fig. 4 (*cy.*) and in section in fig. 2 (*cy.*); each one communicates below with a very much larger inhalant channel (fig. 2, *i.l.*). Thus each subdermal cavity receives the stream of water directly from the exterior through five or six distinct apertures in its roof, and passes it on through a single aperture in its floor into a relatively large inhalant channel. Just as a number of pores lead into one and the same subdermal cavity, so also a number of subdermal cavities lead into one and the same inhalant channel.

(c) The Inhalant Canal System below the Subdermal Cavities.

The large inhalant channels (fig. 2, *i.l.*) into which the subdermal cavities directly lead are comparable to the subcortical crypts described by Sollas (17) in the Tetractinellida, but it is needless to apply a special name to them in Stelospongus. They are merely the larger proximal portions of the inhalant canal system, commencing immediately beneath the ectosome and penetrating deep down into the choanosome.

These larger channels lead into an irregular system of much smaller, more or less lacunar channels, whose ultimate ramifications open into the flagellated chambers (fig. 6); and numerous flagellated chambers open out of one and the same inhalant lacuna.

It must not be supposed that the inhalant canal system is always constant in arrangement; the above description applies to what appears to be a fairly typical case, but there seems to be a good deal of variation, especially with regard to the subdermal cavities and the channels into which they lead.

(D) The Flagellated Chambers.

These are more or less spherical sacs (figs. 6, 7, 10) about 0·04 mm. in diameter, with two wide apertures of about equal size placed at opposite poles, whereby they communicate on the one hand with an ultimate inhalant lacuna and on the other with an ultimate exhalant lacuna. In the same way that several chambers open out of one and the same ultimate inhalant lacuna, so also several may lead into one and the same ultimate exhalant lacuna. Both the inhalant and exhalant apertures of the chambers are usually drawn out into short and relatively wide cameral canaliculi (fig. 10, *i. c. c.*, *e. c. c.*), but I do not think too much importance must be attached to this fact.

(E) The Exhalant Canal System.

The ultimate exhalant lacunæ[1] (fig. 6, *e. l.*), into which the flagellated chambers open usually through the medium of distinct canaliculi, collect together and finally discharge their contents into branches of the oscular tubes. Each oscular tube is a perfectly definite tubular canal about 6 mm. wide, with distinct walls of its own, and leads vertically upwards to a wide osculum situated on the upper margin of the Sponge. The oscular tube itself may readily be dissected out from the surrounding choanosome, from which its walls are very easily separable. Fig. 5 represents a dissection of the oscular tube (*o. t.*) showing its relations to the osculum (*o.*) and the openings into it of a number of larger and smaller branches.

The osculæ are wide, circular openings, about 6 mm. in diameter, placed in a row along the upper margin of the Sponge; their position is indicated in fig. 1 by the letters *o. o. o.*, and in the same figure a portion of an oscular tube (*o. t.*) is seen on the cut surface.

In connection with the exhalant canal system I may here mention certain spherical cavities (fig. 5, *e. c.*) lying in the

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[1] It is impossible to distinguish sharply between a canal and a lacuna; either term might be applied in this case.

neighbourhood of the oscular tube and containing each a single large embryo (*e.*). These cavities appear to be entirely closed and cut off from the remainder of the canal system of the Sponge, but it seems possible that they are really portions of the exhalant canal system, specially modified to serve as receptacles in which the embryos are lodged during a large portion of their development. There are two arguments in favour of this view: (1) The position of the cavities in question, in close proximity to the oscular tubes. (2) The well-known fact that in many Sponges the embryos normally escape from the parent through the exhalant canals[1].

(F) General Remarks on the Canal System.

From the foregoing account it will be evident that the canal system of Stelospongus flabelliformis approaches most nearly to Dr. Vosmaer's third type (18); although, however, several chambers communicate with one and the same ultimate inhalant or exhalant lacuna, the openings of the chambers are provided with short and relatively wide cameral canaliculi. Still the canal system differs little from the ordinary lacunar type so characteristic of the large family Halichondrina (14), and also found occasionally in the Clavulina (14) and other groups.

With regard to other members of the Ceratosa, some have been shown to possess the lacunar type of canal system and some the canalicular type. Professor Schulze (15) has described both these conditions as they exist in different members of the group. Unfortunately, I am unable at present to obtain access to his original papers, but I may quote the following passage from Poléjaeff's work (13) which will sufficiently indicate the state of the case:—" Schulze ascertained, in fact, that while an Aplysina, and on the other hand a Euspongia or Cacospongia, are characterised, in the organisation of their canal system, by comparatively small, round, or pear-shaped flagellated chambers, each possessing

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[1] Ridley and Dendy have figured an embryo escaping through an exhalant canal in Esperella Murrayi (14).

its own narrow inhalant and exhalant canaliculi, and while the ground-mass surrounding these flagellated chambers is always opaque owing to the presence of small granules, the forms like Spongelia and Aplysilla possess no special cameral canaliculi, their large, pouch-shaped flagellated chambers receiving the water from the subdermal cavities directly by means of the pores in their walls, and expelling it also immediately, without the help of any intermediate narrow canals, into large exhalant cavities, the diameter of these latter being usually far larger than that of the exhalant opening of the corresponding flagellated chamber; and that in these latter instances the parenchyma in the zone of the flagellated chambers is devoid of any granules, being lucid and transparent."

Poléjaeff further informs us that "the flagellated chambers of the representatives of the genera Aplysina and Verongia are small, pear-shaped, or rather hemispherical, each provided with one (?) inhalant and one exhalant narrow canaliculus; and again, the surrounding ground-mass is so very rich in granules that the outlines of the cellular elements in the neighbourhood of the flagellated chambers are scarcely distinguishable. On the other hand, the flagellated chambers of an Aplysilla or Ianthella are large and either of regularly elongated form (pouch-shaped) or of quite irregular outline; no special cameral canaliculi are to be discerned; the flagellated chambers receive the water from the subdermal cavities by means of numerous pores in their walls, and expel it by means of a large exhalant aperture; the surrounding ground-mass is clear and transparent. There are, however, amongst the horny Sponges forms uniting these two extreme differences in every direction."

It would appear from my observations that Stelospongus flabelliformis is one of these connecting forms, for although the inhalant and exhalant canaliculi are only very feebly developed, the ground substance, as we shall see later on, is densely charged with minute granules.

Von Lendenfeld (11) has published a good illustration of the lacunar type of canal system, as it occurs in his Euspongia canaliculata, and this species appears to have the clear transparent ground substance usually found in association with eurypylous chambers.

I have endeavoured to show in a previous paper (9) that we cannot draw any hard and fast line between flagellated chambers with and flagellated chambers without special incurrent and excurrent canaliculi, and I believe with Poléjaeff that these two types graduate into one another. I have also stated above that the chambers of Stelospongus usually have short, relatively wide cameral canaliculi, but that we must not lay too much stress upon this fact. Now, according to Poléjaeff, as we have just seen, Schulze describes the flagellated chambers of Euspongia as being provided with special cameral cananiculi and embedded in a granular ground substance, but to judge from Schulze's figure, as copied by Vosmaer (18), the exhalant canaliculi at any rate are only very slightly develoved, and the arrangement of the chambers in Euspongia agrees very closely indeed with that found in Stelospongus.

HISTOLOGY OF THE SOFT TISSUES.

(A) The Ectosome.

The ectosome (fig. 2, *ect.*) forms a relatively thin external layer all over the body of the Sponge. Owing to the presence in it of a large amount of sand, especially abundant in the raised ridges, it is very hard and tough, and forms an excellent protection against the attacks of parasitic crustaceans, worms, &c., to which Sponges are subject.

The outermost portion of the ectosome is formed by an extremely thin and delicate epidermis, which I have succeeded in making out chiefly in the pore-areas, where the sand grains are absent. In preparations such as that represented in fig. 4, one can easily distinguish the nuclei of the epidermic cells (*n. e. c.*) scattered in the transparent, pore-bearing membrane. These nuclei are small granular bodies, round or oval in shape, about 0·0048 mm. in diameter, and in preparations stained with borax carmine they stand out very sharply. I have endeavoured to demonstrate the outlines of the epidermic cells by means of silver nitrate staining, but possibly owing to the fact that I had only spirit material to work with without success. Doubtless this epithelium is continued inwards through the pores to line the subdermal cavities, but I have not succeeded in detecting it here.

A very large proportion of the ectosome is occupied by the sand grains above mentioned, but surrounding these is a considerable quantity of mesodermal tissue.[1] This is for the most part made up of cystenchyme (fig. 13), but stellate mesodermal cells (fig. 12) are also present.

The term cystenchyme has been applied by Sollas (17) to a peculiar form of tissue not uncommonly met with in the ectosome of Sponges. This tissue consists essentially of a number of more or less spherical cells, each provided with a distinct cell wall, and containing a very much vacuolated protoplasm in the interior. The nucleus appears to be suspended in the centre of the cell in a central protoplasmic mass connected with the cell wall by radiating strands of protoplasm. The whole structure resembles very much an ordinary vegetable parenchyma cell. The individual cells are packed more or less closely together, and the spaces between them are filled with a granular or sometimes fibrous substance, which is probably chiefly of an intercellular nature.

In Stelospongus the cystenchyme cells (fig. 13) are oval or subglobular in shape, measuring about 0·024 mm. in diameter, and the nucleus is small and granular. The protoplasmic strands connecting the nucleus with the cell wall are best seen in unstained preparations mounted in glycerine; they are in such seen to form a network, branching and anastomosing inter se. Fig. 14 represents a single cell from such

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[1] I use the term mesoderm here and elsewhere because it is in such very general use amongst spongologists, and not because I believe the tissues thereby designated to be homologous with the mesodermal tissues of other animals.

a preparation; the outlines of the protoplasmic strands are probably much more hard and distinct than in life, owing to the action of the reagents. In balsam preparations (fig. 13), owing doubtless to the greater transparency, the protoplasmic strands are not nearly so distinct.

I may here mention the fact that cystenchyme occurs also in the choanosome of Stelospongus, but to this point I shall recur later on.

This form of tissue, or very slight modifications of it, has been observed in Sponges of very divers groups. Sollas (16, 17) has described it in Tetractinellida (Pachymatisma Johnstoni), Poléjaeff (13) in Ceratosa (Cacospongia vesiculifera), and Ridley and Dendy (14) in Clavulina (Latrunculia apicalis).

The stellate mesodermal cells of the ectosome appear to be thoroughly typical. They may be seen investing the grains of sand in a kind of delicate network, the individual cells being mutually connected by long slender processes (fig. 12). The body of the cell is somewhat granular and the nucleus is oval and of moderate size.

I have not observed any definite arrangement of the cystenchymatous and stellate tissues with regard to one another, nor have I any reason to suppose that such exists.

(B) The Choanosome.

I propose to consider the histological characters of the choanosome under the following heads: (1) The walls of the inhalant and exhalant canals. (2) The walls of the embryo-containing cavities. (3) The walls of the flagellated chambers. (4) The general mass of mesoderm in which the chambers and canals are embedded. (5) The spongoblasts and other mesodermal cells surrounding the skeleton fibres. This arrangement is a purely arbitrary one, and I have adopted it merely as a matter of convenience, in view of the necessity of some definite plan to go upon. It is a matter of no small difficulty to classify satisfactorily the various forms of tissues and cell-elements which occur in any given Sponge.

(1) The Walls of the Inhalant and Exhalant Canals.

It will be convenient to give these the first consideration on account of their close relationship to the ectosome, from which they cannot be sharply separated.

The larger or proximal portions of the inhalant canal system are provided with special walls of mesodermal tissue. The true nature of this lining membrane is difficult to determine. In sections it is seen to consist of a very much vacuolated gelatinous tissue, composed more or less of cystenchyme, but in parts becoming fibrous.

No doubt even the larger portions of the inhalant canal system are also provided in life with a very delicate epithelial lining, forming the outermost layer of their walls, but this I have not been able to detect, possibly owing to the manner in which the entire gelatinous lining membrane shrivels up in spirit.

The ultimate inhalant lacunæ, which open into the flagellated chambers as above described, have no special mesodermal walls; but here the nuclei of a delicate, flattened, lining epithelium can be easily detected in thin sections (fig. 6, *n. e. c.*), and occasionally a large cystenchyme cell may be seen embedded in the choanosome immediately beneath this epithelium.

The ultimate exhalant lacunæ, into which the flagellated chambers discharge their contents, have, like the ultimate inhalant lacunæ, no special mesodermal walls, but are lined by a delicate flattened epithelium, whose nuclei can be detected in thin sections. The larger exhalant channels, or oscular tubes, are, however, provided with most distinct walls, which can be dissected away from the underlying tissues with great ease (fig. 5). These walls are membranous and fairly tough, and they are continued from the oscular tube itself along its various larger branches as a distinct lining membrane.

The wall of the oscular tube is seen in transverse section to be made up of the following layers from within outwards:

(*a*) A thick rather irregular layer of very much vacuolated gelatinous tissue, composed of anastomosing strands of transparent jelly-like substance, containing small nuclei here and there. It is doubtless owing to the presence of this layer of very delicate tissue that the wall of the oscular tube can be so readily peeled off from the underlying structures.

(*b*) A much thinner layer of deeply-staining fibrous tissue, in which the fibres are closely packed and arranged circularly around the oscular tube. Judging from its position and the arrangement of its component fibres, it seems probable that this layer may be muscular, and its fibres myocytes (Sollas, 17), which by their power of contraction serve to regulate the diameter of the oscular tube. The wall of the oscular tube is smooth on the interior, and devoid of diaphragms or special circular sphincter muscles, such as occur in many Sponges. (Diaphragms are well developed in the genus Spirastrella, and circular sphincter muscles in Quasillina; both doubtless serve the same function. The condition of Stelospongus in this respect is comparable to that of Ridleia (cf. 9)).

(*c*) A continuous layer, only about one cell thick, of cystenchyme. This layer may best be studied by peeling off portions of the wall of the oscular tube and preparing and mounting them without embedding, for cystenchyme appears to be a very delicate tissue, which suffers greatly in the latter process.

In preparations stained with borax carmine, and mounted in the usual way, the cystenchyme is seen to form a continuous layer, about one cell thick, of closely packed cells which have become somewhat polygonal from mutual pressure. Between the cells a deeply-staining, granular, intercellular substance is present, and the structure of the individual cells is the same as that which I have already described in the case of the ectosomal cystenchyme.

This layer is at first sight deceptively like a layer of large, flattened, epithelial cells, and I at first mistook it for such; but the characters of the component cells made me doubt if this could be so, and on cutting sections its real nature became readily apparent. The individual cells measure about 0·03 mm. in diameter.

I have no doubt that the wall of the oscular tube is completed on the inside by a delicate flattened epithelium, but I have not succeded in demonstrating its presence.

(2) The Walls of the Embryo-containing Cavities.

I have above stated the reasons for regarding the cavities in which the embryos are lodged as specialised parts of the exhalant canal system. Whether this view be adopted or not—and it is still an open question—the structure of their walls may be most conveniently treated of in this place, although I shall be obliged to refer again to this portion of my subject when speaking of the development.

The only ovum which I have observed previous to the commencement of segmentation lies in a small cavity, about 0·1 mm. in diameter, situate in the innermost part of the gelatinous layer of the wall of an oscular tube. This cavity has a special wall, about 0·0144 mm. thick, composed of fibrous tissue with elongated nuclei, similar to that represented in fig. 15, but not so strongly developed. I have not detected a lining epithelium, but some of the nuclei which are observable in the outermost part of the wall may possibly belong to a delicate epithelial layer similar to that which lines the smaller branches of the canal system, and which must almost certainly occur here also.

The large embryo-containing capsules now to be described are probably developed simply by growth of the small capsules containing the ova. The walls of these large capsules are, however, very much more highly differentiated than those of the ovum-containing capsules, and consist of two very distinct layers, (*a*) a fibrous layer, and (*b*) a lining epithelium. The fibrous layer of the wall (fig. 15) is very dense next to the lining epithelium, but further in it becomes looser and is broken into by large lacunar spaces. It is composed of circularly arranged fibres each consisting of a greatly elongated fusiform granular cell, with a deeply-staining oval nucleus in the centre. The fibres are so densely packed in the outer part of the layer next to the lining epithelium that the outlines of the individual cells can no longer be distinguished, but further in the cells lie farther apart and the tissue partakes more of the nature of a compact stellate mesoderm.

The lining epithelium of the embryo capsule (fig. 16) is very peculiar and, so far as I am aware, entirely different from anything which has hitherto been described in Sponges. It is composed of a single layer of enormous polygonal cells. These cells, although flattened, are thick, each one measuring from about 0·072 mm. in diameter for the youngest embryo examined up to 0·12 mm. for older ones, and about 0·024 mm. in thickness. The body of the cell is finely granular, and each contains in its centre a very large, flattened, oval nucleus containing a number of deeply-staining granules. In the largest cells the nucleus may be seen to be undergoing division, doubtless preparatory to the division of the whole cell. Thus, in fig. 16 the nucleus of one of the cells has acquired a horseshoe shape, the two arms of the horse-shoe being nearly separated from one another, and in another cell the division is complete and the cell contains two nuclei. I have observed no karyokinetic figures.

In transverse sections the outer surfaces of the cells are frequently, but by no means always, seen to be indented (fig. 20). These indentations would appear to correspond in some way to the upper portions of the cells of the outer layer (ectoderm) of the embryo, which in life are closely connected, as we shall see later on, with the epithelial layer of the embryo capsule.

In transverse sections also the body of the cell is seen to be granular throughout, but the granules are very much finer around the nucleus than towards the periphery of the cells (figs. 17, 21). The cell always has a definite bounding wall on its outer, and sometimes also on its inner, surface; but frequently its inner surface, which in life is pressed against the fibrous layer of the embryo capsule, exhibits no such wall (fig. 21).

In sections the nucleus sometimes appears solid (fig. 21), and sometimes as a hollow vesicle provided with a distinct wall and enclosing a granular substance (fig. 17).

These epithelial cells very readily become detached from the underlying fibrous layer of the capsule, and sometimes remain adherent to the embryo when the latter is removed from the parent Sponge (fig. 18). In sections, owing to the treatment undergone, they very often appear entirely isolated, having been torn both from the embryo and from the fibrous layer of the capsule, or they may remain adherent to the embryo while separated from the fibrous layer, or to the fibrous layer while separated from the embryo. Owing to its relationship to, and intimate connection with, the outer layer of cells of the embryo (and for certain other reasons) I believe this peculiar lining epithelium of the embryo capsule to be nutritive in function, but to this point I shall return again when treating of the development.

It must be borne in mind that there is no evidence actually to prove that these large epithelial cells belong to the mother Sponge and not to the embryo itself, but the latter hypothesis seems to me so improbable that I shall not consider it any further.

(3) The Walls of the Flagellated Chambers.

The walls of the flagellated chambers are, of course, composed of collared cells, but these cells exhibit certain very peculiar and interesting details in structure.

In his article on Sponges in the 'Encyclopædia Britannica' (17) Sollas has shown that in certain Sponges the collar of the collared cells (or choanocytes, as he terms them) are united together at their margins by a continuous membrane which forms a kind of inner lining to the flagellated chamber. He says, "In Tetractinellida, and probably in many other Sponges—certainly in some—the collars of contiguous choanocytes coalesce at their margins so as to produce a fenestrated membrane, which forms a second inner lining to the flagellated chamber. The presence of this membrane enables us readily to distinguish the excurrent from the incurrent face of the chamber, since its convex surface is always turned towards the prosopyle."[1]

This short passage, and a not very satisfactory woodcut accompanying it, comprise all the information which we as yet possess concerning this very remarkable and important structure, but doubtless further details will be given in Professor Sollas's forthcoming report on the "Challenger," Tetractinellida. Meantime it has been my good fortune to be able to demonstrate, beyond the possibility of a doubt, the existence of this connecting membrane, which I propose to call Sollas's membrane, in Stelospongus.

In Stelospongus the collared cells are arranged at about equal distances all around the flagellated chamber, but they are interrupted at the proximal pole by the inhalant, and at the distal pole by the exhalant aperture (figs. 6, 10). They are not all of the same size; they are largest around the inhalant aperture, gradually diminishing towards the exhalant aperture, around which they are smallest (figs. 6, 10). Each cell (figs. 8, 9) consists of a cylindrical "collum" or neck, with a large oval nucleus lying in its slightly expanded base (the body of the cell). The collum projects freely into the chamber, and gives support to the delicate membranous collar. The collar is rather longer than the collum, and, though necessarily of the same diameter as the latter at its base, considerably wider at its summit. Thus, the whole cell, including the collar, has somewhat the shape of a dice-box, being narrower in the middle than at the two ends. I have not been able to trace any definite outline to the body of the cell, which is embedded in the highly granular ground substance, but the nuclei are always very conspicuous as relatively large, deeply-staining, oval, granular bodies, sometimes apparently with a nucleolus (fig. 8).

The flagella cannot be detected in my preparations, being entirely shrivelled up, or possibly retracted, when the Sponge was placed in spirit. Certain granular bodies, sometimes visible on the collars and represented in fig. 8 (*g.*), may possibly

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[1] = inhalant aperture.

represent the shrivelled remnants of flagella, but it is extremely doubtful. The largest collared cells of a chamber measure about 0·0096 mm. in total height (including the collar), and the nucleus is about 0·0032 mm. in its largest diameter.

The margins of the collars are all connected together by a continuous, very delicate membrane, Sollas's membrane, which lies in a plane at right angles to the long axis of the collared cell. This membrane is seen in thin vertical sections as a fine thread running from collar to collar, as shown in fig. 8, which represents an actual preparation. If the section, however, instead of being taken at right angles to Sollas's membrane, happens to be taken in a plane more or less parallel to it, then the membrane frequently appears as an irregular network of delicate transparent strands, shrivelled up and distorted by the action of the reagents, but easily recognisable lying within the chamber. Fig. 7 represents such a section.

It might perhaps be thought that if Sollas's reticulate membrane exhibits its true form and relationships in vertical sections it ought also to do so in horizontal sections; but this by no means follows, for in horizontal sections the membrane is severed from the collars of the cells upon which it is naturally supported, and being no longer kept in position by these is at liberty to shrivel up, which it promptly does.

Fig. 9 is a diagram representing what I believe to be the natural relationships of the parts under discussion.

From what has been said of the sizes and arrangement of the collared cells in each chamber it will be seen that the membrane uniting their margins, Sollas's membrane, will not run parallel to the wall of the chamber, but will be furthest from it at the proximal or inhalant pole, and nearest to it at the distal or exhalant pole. This is actually the case, for at the proximal pole the membrane is widely separated from the wall of the chamber, while at the distal pole the two become confluent, as shown in the diagram, fig. 10. Hence the membrane has the form of a hollow cup, whose concavity is turned towards the exhalant aperture of the chamber.

It is obvious that Sollas's membrane divides the cavity of the flagellated chamber into two portions, (1) a central portion into which the flagella project, and (2) a peripheral portion lying between the collared cells. It is further clear that the stream of water kept up by the movements of the flagella can pass only through the central portion of the chamber. It may give access to the peripheral space by means of gaps between the collared cells around the inhalant aperture, but as it has no means of egress this would be of no consequence. In short, the membrane may serve to facilitate the flow of the water by diminishing the friction, for it is evident that the water will flow more easily over a smooth membrane than if it had to run in and out between the collared cells. It has been pointed out to me by Sir James Hector that Sollas's membrane may also play some part in determining the direction of the current of water, but this is a mechanical problem which I am at present unable to solve.

Now that attention has once been directed to its existence this membrane will probably be found to be very generally present in Sponges. I may state here that I have already detected it in Halichondria panicea, of the minute anatomy of which species I hope to be able to give an account before very long, so that it is now known to exist in three groups, Tetractinellida, Ceratosa, and Halichondrina.

(4) The General Mass of Mesoderm in which the Chambers and Canals are Embedded.

The flagellated chambers are pretty closely packed together in the choanosome, and together with the various branches of the canal system make up the greater part of its bulk. Hence the amount of fundamental or ground tissue in which they are embedded is not very great. What there is is packed full of minute, highly refringent granules (figs. 6, 7, 8, 9, 10), fairly evenly distributed through it, and resembling in size and general appearance the intracellular granules of some of the forms of tissue already described (e. g. the fibrous cells which form the inner layer of the embryo capsules).

Embedded in this granular matrix may be observed, scattered here and there, small nucleated cells of irregularly rounded outline (figs. 6, 10, *m. c.*), doubtless the amœboid cells of authors. This ground tissue appears to agree thoroughly with that which Schulze has described (15) as existing in Euspongia.

(5) The Spongoblasts and other Mesodermal Cells surrounding the Skeleton Fibres.

In most parts the skeleton fibres are surrounded by a sheath of ordinary stellate and slightly fibrous connective tissue. In some places, however, doubtless those in which growth of the fibre is going on and active secretion is taking place, the stellate mesodermal cells are specially modified as spongoblasts or glandular cells whose function it is to secrete the spongin of which the horny fibre is composed. In Stelospongus flabelliformis these spongoblasts have the form indicated in fig. 11, and they form a layer one cell thick around the fibre. Each spongoblast is a somewhat club-shaped, slender, elongated, granular mesodermal cell, about 0·048 mm. in length. One end is drawn out into a long, gradually tapering neck, and the other broader end is usually rounded off (but sometimes stellate), and contains a spherical nucleus. The whole cell is frequently more or less bent or contorted; its long axis, however, always lies approximately at right angles to the surface of the fibre against which its narrow end abuts. There is commonly, if not always, a layer of ordinary stellate mesoderm outside the layer of spongoblasts, and it is easy to see that the spongoblasts themselves are simply slight local modifications of the ordinary stellate type of cell, their origin being still sometimes plainly indicated by the stellate form of the broad end (fig. 11).

The spongoblasts thus described are practically identical with those observed and figured by Schulze in Euspongia (15), with the exception that they are very much more elongated.

NOTES ON THE DEVELOPMENT.

My observations on the embryology of Stelospongus are as yet necessarily very imperfect, for all the embryos which I have yet found are in pretty much the same stage of development. Of this particular stage there is, however, an abundant supply, and it presents such very remarkable features that I do not hesitate to give a detailed account of it in this place, hoping at the same time to be able to extend my observations at a later date.

Historical Account.

In connection with this portion of our subject it is necessary to bear in mind in the first place some very remarkable observations of Mr. Carter's (1, 2, 3, 4, 5), which, though published many years ago by such a careful observer, appear to have almost entirely sunk into oblivion. The gist of the observations referred to is that in the developing gemmule (seed-like body, Carter) of Spongilla the flagellated chambers (ampullaceous sacs, Carter) are formed each from a single large amœboid mesodermal cell whose contents break up into a number of small cells (germs or ovules, Carter) which arrange themselves round a central cavity and develope into collared cells.

A few quotations will suffice to illustrate this point. Mr. Carter (4) says that Spongilla "is charged towards the base with a number of seed-like bodies of a globular shape, each of which consists of a coriaceous membrane enclosing a number of delicate, transparent spherical cells, more or less filled with ovules and granular matter. . . . It has also been shown that at an early period of development the spherical, which we shall henceforth call 'ovibearing,' cells are polymorphic—identical but for the ovules, with the ordinary sponge-cells—and surrounded by a layer of peculiar cells equally polymorphic, which I have conjectured to be the chief agents engaged in constructing the capsule. . . . . The seed-like body presents a hole, which we shall call the 'hilum.' . . . .

The contents issue through the hilum under the form of a gelatinous mass, in which the ovibearing cells and their contents appear to be embedded entire. . . . . The ovibearing cells are developed into spherical ampullaceous sacs, communicating with the afferent canals. . . . . The ovibearing cells do not burst and allow their contents to become indiscriminately scattered through the gelatinous mass in which they are embedded, but each becomes developed separately and entire in the following way, viz. the ovules and granules of the ovibearing cell subside into a granular mass by the former losing their defined shape and passing into small monociliated and uniciliated sponge-cells; this mass then becomes spread over the interior surface of the ovibearing cell, leaving a cavity in the centre into which the cilia of the monociliated sponge-cells dip and keep up an undulating motion; meanwhile an aperture becomes developed in one part of the cell which communicates with the adjoining afferent canal, and thus the ovibearing cell passes into an ampullaceous spherical sac."

It is astonishing how such a precise account, coming from the pen of so careful an observer as Mr. Carter, has received so small a share of attention from subsequent writers. I do not see any reason to doubt the accuracy of Mr. Carter's statements, and I shall presently endeavour to show that the flagellated chambers develope in precisely the same manner in the embryos of Stelospongus.

Two other authors, viz. Metschnikoff and Goette, have described a mode of development of the flagellated chambers which appears to me to agree pretty closely with that observed by Mr. Carter in the gemmules of Spongilla, and by myself in the embryos of Stelospongus. Unfortunately, I am unable to obtain access to the original papers of either of these authors, and I am obliged therefore to content myself with the very brief abstracts, fortunately accompanied in the first case by figures, given by Vosmaer (18).

Metschnikoff (12) describes and figures the embryo of Halisarca dujardini at a certain stage as consisting of an outer layer of columnar epithelium and a few "rosette-cells" in the interior. The origin of these so-called "rosette-cells" is unknown; from the figures, copied by Vosmaer, they appear to consist each of a spherical ball composed of a few small cells arranged around a small central cavity. The rosette-cells increase until finally they fill the whole cavity of the embryo. Metschnikoff regards the rosette-cells as mesoblastic structures, and he states also that amœboid cells wander in amongst them from the epiblast; the canals commence as isolated spaces in in the mesoblast. Vosmaer gives no further account, but from what he says, and from the figures, it seems very probable that the so-called rosette-cells are the young flagellated chambers, and that they have themselves been formed each from a single large amœboid cell derived from the epiblast.

Goette (10) gives a long account of the development of Spongilla, and Vosmaer tells us in his abstract that "Die Geisselkammern entwickeln sich getrennt von einander und von anderen Hohlräumen 'vermittelst einer Knospenbildung einzelner Zellen.'"

DEVELOPMENT OF STELOSPONGUS FLABELLIFORMIS.

(A) The Ovum.

The ovum appears in section as a somewhat oval cell lying in a fibrous capsule as described above. The body of the ovum is granular and deeply staining. At one pole there is a large oval nucleus with a very definite wall, and right up against the wall, at the outer pole of the nucleus, there lies a small, spherical nucleolus. The nucleus does not contain nearly so many granules in proportion to its size as the body of the ovum, but there is a quantity of coarsely granular material chiefly aggregated towards the pole, remote from the nucleolus. The nucleolus stains deeply, and is almost, if not quite, homogeneous. The longer diameter of the ovum measures 0·076 mm., of the nucleus 0·024 mm., and of the nucleolus 0·0048 mm.

(B) The Embryos.

As already stated, the embryos are all in pretty much the same stage of development, although varying in diameter from about 3 mm. to nearly 5 mm. The immense size of these embryos as compared with those of other Sponges has already been noticed by Mr. Carter[1] (7), but he says scarcely a word about their structure.

While out dredging with Mr. Wilson I picked a number of these embryos out of the living Sponge with forceps, and tried the effect of at once placing in fresh sea-water, but I could detect no signs of motion of any kind.

All the embryos were solid, with the exception of one or two of the smaller ones. These when examined in spirit appeared to be hollow, but they were damaged, and I believe the hollow character was a post-mortem condition[2] due to the escape or shrivelling up of the very delicate gelatinous, or probably in the youngest stages more or less liquid, tissue from the interior. I shall therefore not consider them apart from the remainder.

When the surface of the embryo is examined with a pocket lens it exhibits a minutely punctate appearance, due to the presence of an immense number of shallow pits, somewhat polygonal in outline, and separated from each other by low ridges (fig. 18). Sections show that each one of these pits is the imprint of one of the large epithelial cells of the embryo capsule. The pittings were present, in parts at any rate, on the smallest embryo examined, but they were not nearly so well marked as on the older embryos. All my further observations were conducted by means of sections.

The embryo consists of an outer layer of rather large, closely packed cells enclosing a mass of clear, transparent, jelly-like substance, in which immense numbers of amœboid wandering

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[1] Mr. Carter says: "The largest embryo I have seen in the marine Sponges is that of Stelospongus flabelliformis, Cart., ... where it is spherical and one sixth of an inch in diameter."

[2] Cf. Quasillina.

cells are embedded. The outer layer, or ectoderm, consists of a single layer of large, sac-shaped or somewhat flask-shaped cells (figs. 19, 20, 21, 22) measuring about 0·024 mm. in length. The narrower portion, or neck, of the cell is on the outside of the embryo, and the swollen portion projects inwards into the gelatinous intercellular substance, and from its inner extremity frequently sends out a few very short, slender pseudopodial processes (figs. 19, 20, 21, 22). These processes may possibly serve to transmit nutriment to the cells in the interior, or they may simply indicate a tendency in the ectodermal cells to become amœboid. The body of the cell is coarsely granular, but less so in the neck than in the swollen portion. The greater part of the neck is, however, occupied by a large, spherical nucleus, which appears to consist of a hollow vesicle containing a few deeply-staining granules. I have observed no nucleolus. The nuclei are all arranged at just about the same level, so that the nuclei of adjacent cells form a continuous row, which is a very conspicuous feature in sections of the embryo.

Frequently the outer end of the neck of the ectodermal cells may be seen to be drawn out into a short, slender, protoplasmic process, which extends to the outer surface of one of the large investing epithelial cells (fig. 21), and attaches itself to the latter. Thus the ectodermal cells of the embryo often appear to be suspended from the outer surfaces of the investing epithelial cells by short protoplasmic processes, as shown somewhat diagrammatically in fig. 21. Judging from the number seen in a single transverse section, it would appear that each of the large epithelial cells may have a hundred or more sac-shaped ectodermal embryonic cells hanging from its outer surface.

The unusual length of time during which the embryo remains within the mother Sponge, and the great size to which it attains, necessitate some special arrangement whereby it can be nourished. The peculiar relation of the ectodermal cells of the embryo to the investing epithelium, and the very unusual character of the latter, cause me to believe that the investing epithelium has for its function the nutrition of the embryo, and that this is effected by the absorption of nutriment through the elongated necks of the ectodermal cells.

Some of the ectodermal cells, however, exhibit no prolongations of the neck, but are smoothly rounded off at the free end, and such cells may form a continuous layer over a considerable area. In most sections, however, owing to the forcible displacement of the nutrient epithelial cells and the rupture of the delicate connections between them and the ectodermal cells, the latter appear as if broken off at their outer ends, just outside the nucleus (figs. 19, 20, 22).

The entire mass of the embryo within the ectodermal layer is made up of a clear, jelly-like matrix, in which immense numbers of large, amœboid wandering cells are embedded (figs. 19, 22). These cells appear somewhat larger than the ectodermal cells, but I shall show presently that there is very strong reason to believe that they are simply ectodermal cells which have left their places in the outer layer, and, becoming amœboid, wandered into the central jelly. Between the large amœboid cells very delicate branching stellate cells may sometimes be seen (fig. 22, *st. c.*).

The amœboid cells may put out pseudopodia in all directions, but often they appear to be radially elongated and more or less bipolar. I think my sections, and especially such as that represented in fig. 22, show conclusively that the amœboid cells are derived from the ectodermal layer. They agree firstly in all essentials with the cells of the latter, and in those parts where the ectodermal cells, having the clearer, outer end of the neck evenly rounded off, present a characteristic feature, a precisely similar clear, rounded-off neck may often be seen in the amœboid cells immediately beneath the ectoderm. In fig. 22 two cells appear just leaving the ectodermal layer and becoming amœboid by the emission of pseudopodia. The amœboid cells are from the first highly granular and, at what I believe to be an early stage of the proceedings, each one has a spherical nucleus resembling that which occurs in the ectodermal cells. Sometimes the amœboid cells lying near the outside of the embryo have two or three nuclei (fig. 22), and very rarely also even the ectodermal cells appear to have two nuclei (fig. 20). At a later stage (fig. 23) the entire amœboid cell is seen to have become indistinct in outline, and in place of one large cell we have an aggregation of very minute spherical bodies about 0·0025 mm. in diameter, each with a dark spot in its centre; but each aggregation still retains the form of the original amœboid cell. In the same sections which exhibit this condition many of the amœboid cells appear to have become rounded, their contents having arranged themselves around a central cavity (fig. 23, *f. c.*), so that we have a hollow chamber lined by small, spherical cells. These chambers I believe to be the young flagellated chambers. They are certainly very different in structure from the flagellated chambers of the adult Sponge, and only about half the size, measuring about 0·024 mm. in diameter, but the differences are easily accounted for by their embryonic condition. I have not been able to trace the development of the chambers any further, nor is it to be expected that the collars and flagella would be developed before the young Sponge was set free and required them.

Coincidently with the formation of the flagellated chambers in the manner thus described, a slit-like invagination appears on the surface of the young Sponge, and it is chiefly, if not solely, around this invagination that chamber formation takes place. This invagination is probably the commencement of a communication between the chambers and the exterior. Unfortunately, I have only obtained a single embryo which is sufficiently advanced to show the formation of the flagellated chambers and the slit-like invagination from the exterior, but I see no good reason for doubting the normality of the phenomena above described.

The mode in which the embryos of Stelospongus escape from the parent is still an enigma. It may be that by further increase in size they rupture the walls of the oscular tubes in whose immediate proximity they lie, and are then forcibly ejected with the outgoing stream of water; or it may be that the Sponge dies down in the winter, and that the embryos are then released by the decay of the maternal tissues.

I do not think it advisable at present to enter into any speculations with regard to the general significance of the development of Stelospongus, but prefer to wait for more light on the subject.

In conclusion, I have to express my cordial thanks to Professor Howes, of the Royal School of Mines, for kindly undertaking to correct the proof-sheets of this paper in my absence from England.

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(3) Carter.—"Notes on the Infusoria of the Island of Bombay," No. 1, "Organisation" (plate vi, fig. 41), 'Ann. and Mag. Nat. Hist.,' ser. 2, vol. xviii, pp. 115, 221.

(4) Carter.—"On the Ultimate Structure of Spongilla, and Additional Notes on Freshwater Infusoria," 'Ann. and Mag. Nat. Hist.,' ser. 2, vol. xx, p. 21.

(5) Carter.—"On the Nature of the Seed-like Body of Spongilla, &c.," 'Ann. and Mag. Nat. Hist.,' ser. 4, vol. xiv, p. 97.

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(10) Goette.—"Untersuchungen zur Entwickelungsgeschichte von Spongilla fluviatilis," 'Abhandlungen zur Entwickelungsgeschichte der Thiere, III.'

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(14) Ridley and Dendy.—'Report on the Monaxonida Dredged by H.M.S. "Challenger."'

(15) Schulze.—"Untersuchungen über den Bau und die Entwicklung der Spongien," 'Zeitschr. für wiss. Zool.,' xxx, et seq.

(16) Sollas.—"The Sponge-fauna of Norway," 'Ann. and Mag. Nat. Hist.,' ser. 5, vol. ix, p. 141.

(17) Sollas.—Article, "Sponges," 'Encyclopædia Britannica,' edition ix.

(18) Vosmaer.—"Spongien (Porifera)," 'Bronn's Klassen und Ordnungen des Thierreichs,' vol. ii.

EXPLANATION OF PLATES XXX, XXXI, XXXII, & XXXIII,

Illustrating Mr. Arthur Dendy's paper, "Studies on the Comparative Anatomy of Sponges," II, "On the Anatomy and Histology of Stelospongus flabelliformis, Carter; with Notes on the Development."

(*The following Explanation of the Lettering applies to all the Figures.*)

a. c. Amœboid cell in the embryo. *c.* Collar of collared cell. *c. c.* Collared cell. *c. e. l.* Cell of external layer (ectoderm) in the embryo. *ch.* Choanosome. *col.* Collum or neck of collared cell. *cy.* Cystenchyme. *e.* Embryo. *e. c.* Embryo capsule. *e. c. c.* Exhalant cameral canaliculus. *ect.* Ectosome. *e. l.* Exhalant lacuna. *e. l. c.* External layer of cells (ectoderm) of the embryo. *e. o.* exhalant opening of flagellated chamber. *f.* Skeleton fibre. *f'.* Skeleton fibre projecting at the surface of the Sponge. *f. c.* Flagellated chamber. *fl.* Flagellum of collared cell. *g.* Granule on the margin of the collar of the collared cell. *i. c. c.* Inhalant cameral canaliculus. *i. l.* Inhalant lacuna or channel. *i. o.* Inhalant opening of flagellated chamber. *m. c.* Mesodermal cell. *n.* Nucleus. *n. c. c.* Nucleus of collared cell. *n. e. c.* Nucleus of epithelial cell. *nut. c.* Nutrient epithelial cell from the lining of the embryo capsule. *nut. e.* Nutrient epithelium from the lining of the embryo capsule. *o.* Osculum. *o. t.* Oscular tube. *p.* Pore. *p. a.* Pore-area. *p. f.* Primary fibre of skeleton. *pt.* Pit or depression on the surface of the embryo, caused by a nutrient epithelial cell. *r. b.* Deeply staining, radiately fibrous, globular bodies of unknown function, probably parasitic organisms. *r. m.* Reticulate membrane in flagellated chamber, Sollas's membrane. *s. f.* Secondary fibre of skeleton. *s. g.* Sand grain. *spb.* Spongoblast. *st. c.* Stellate cell in the embryo.

PLATE XXX.

Stelospongus flabelliformis.

Fig. 1.—Specimen of Stelospongus flabelliformis, from which a portion of one side has been cut off. Natural size.

Fig. 2.—Outer portion of a section at right angles to the surface of the Sponge, showing the relations of the ectosome (*ect.*) to the choanosome (*ch.*), and the proximal portions of the inhalant canal system commencing with the pores (*p.*).

Fig. 3.—A small portion of the skeleton, showing the primary fibres (*p. f.*) and the secondary fibres (*s. f.*).

PLATE XXXI.

Stelospongus flabelliformis.

Fig. 4.—A small portion of the ectosome, removed from the surface and examined from above as a transparent object after staining with borax carmine, showing the pores (*p.*) arranged in pore-areas (*p. a.*); the cystenchymatous tissue (*cy.*) lying beneath is seen through the transparent epidermis. Drawn under Zeiss's C, ocular 2.

Fig. 5.—A solid section, showing the oscular tube (*o. t.*) partially dissected out, with the openings of its various branches; an osculum (*o.*) and two embryos (*e.*). On the right of the oscular tube are two of the embryo capsules (*e. c.*) from which the embryos have been removed. × 2.

Fig. 6.—Portion of a section through the choanosome, showing the relations of the ultimate inhalant lacunæ (*i. e.*), the flagellated chambers (*f. c.*) and the ultimate exhalant lacunæ (*e. l.*). Drawn under Zeiss's F, ocular 2.

Fig. 7.—Section through a single flagellated chamber, showing Sollas's membrane (*r. m.*) as it very often appears in ordinary preparations. Drawn under Zeiss's F, ocular 2.

Fig. 8.—Small portion of an actual vertical section through the wall of a flagellated chamber, showing three collared cells connected together at the margins of the collars by a delicate membrane, seen in section (*r. m.*), Sollas's membrane. The granular bodies (*g.*) on the collars (*c.*) may possibly represent the last remnants of shrivelled-up flagella. Drawn under Zeiss's F, ocular 2.

PLATE XXXII.

Stelospongus flabelliformis.

Fig. 9.—Diagram of a portion of the wall of a flagellated chamber, showing the various parts of the collared cells and their relations to the reticulate membrane (Sollas's membrane, *r. m.*) which connects together the margins of the collars.

Fig. 10.—Diagram of a section through a flagellated chamber, passing through the inhalant (*i. o.*) and exhalant (*e. o.*) openings, showing the arrangement of the collared cells (*c. c.*) and the relations of the inhalant (*i. l.*) and exhalant (*e. l.*) lacunæ, and inhalant (*i. c. c.*) and exhalant (*e. c. c.*) cameral canaliculi.

Fig. 11.—A group of spongoblasts (*spb.*), showing their form and relations to the skeleton fibre (*f.*). Drawn under Zeiss's F, ocular 2.

Fig. 12.—Portion of a plexus of stellate mesodermal cells from around a grain of sand in the ectosome. Drawn under Zeiss's F, ocular 2.

Fig. 13.—Cystenchyme from the ectosome, from a section stained with

borax carmine and mounted in Canada balsam. Drawn under Zeiss F, ocular 2.

Fig. 14.—A single cystenchyme cell from the ectosome, showing the nucleus (*n.*) suspended in a network of protoplasmic threads. From a preparation mounted in glycerine without embedding. Drawn under Zeiss's F, ocular 2.

Fig. 15.—Portion of the fibrous layer of an embryo capsule. The right hand side of the figure corresponds to the inner portion of the layer, next to the lining epithelium. Drawn under Zeiss's F, ocular 2.

PLATE XXXIII.

Stelospongus flabelliformis.

Fig. 16.—Group of large nutrient epithelial cells, from the lining epithelium of an embryo capsule. Drawn under Zeiss's D, ocular 2.

Fig. 17.—Vertical section of one of the large nutrient epithelial cells from the lining epithelium of an embryo capsule. Drawn under Zeiss's F, ocular 2.

Fig. 18.—Portion of the surface of a large embryo, as seen with a hand lens, showing the shallow pits on the surface (*pt.*), and on the left of the figure the nutrient epithelium from the embryo capsule (*nut. e.*) still adherent.

Fig. 19.—Portion of a radial section of an embryo, showing the ectodermal layer of cells (*e. l. c.*), and the large amœboid cells (*a. c.*) embedded in the inner jelly-like mass. (The transparent gelatinous matrix is not represented.) Drawn under Zeiss's C, ocular 2.

Fig. 20.—Outer portion of a section similar to that represented in Fig. 19, more highly magnified, with the remains of a nutrient epithelial cell (*nut. c.*) still visible. The section corresponds to a transverse section through a single one of the shallow pits represented in Fig. 18.

Fig. 21.—Vertical section through one of the large nutrient epithelial cells (*nut. c.*), with the ectodermal cells of the embryo (*c. e. l.*) attached to its inner surface by means of slender prolongations of their necks. Drawn under Zeiss's F, ocular 2.

Fig. 22.—Small portion of a section through an embryo, showing how the ectodermal cells (*c. e. l.*) become amœboid (*a. c.*), and migrate inwards. Drawn under Zeiss's F, ocular 2.

Fig. 23.—Portion of a section through the interior only of the most advanced embryo, showing how the large amœboid cells (*a. c.*) break up into a great many minute spherical cells, which arrange themselves around a central cavity and form the young flagellated chambers (*f. c.*). Drawn under Zeiss's F, ocular 2.

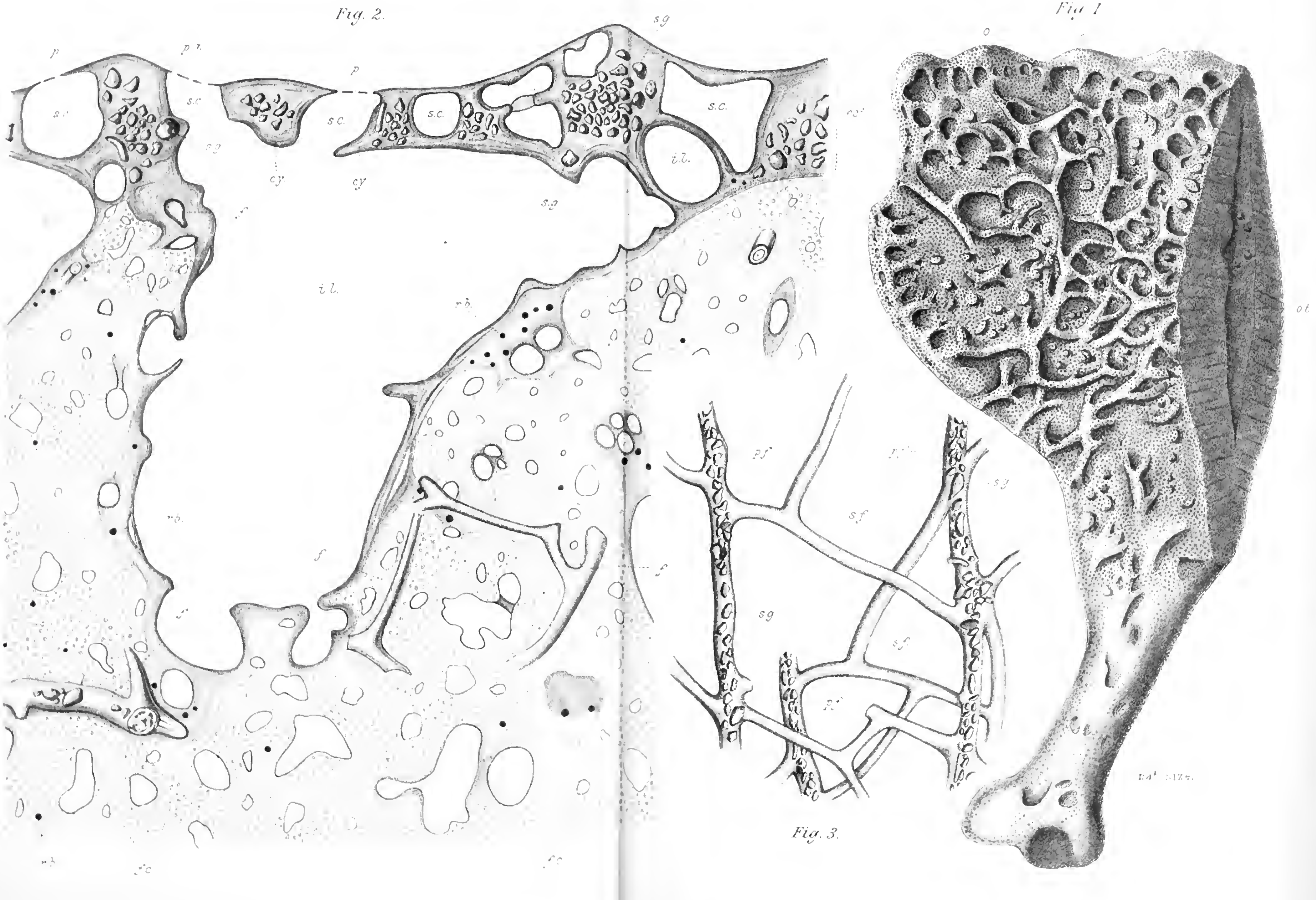

Fig. 2.

Fig. 1

Fig. 3.

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Fig. 4

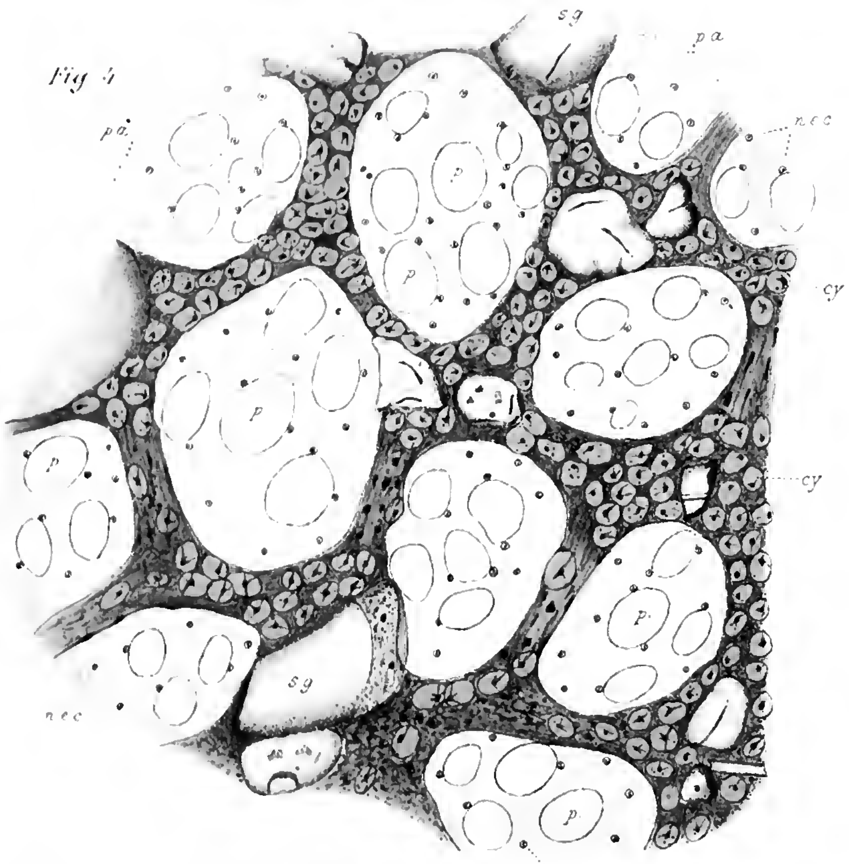

Fig. 5
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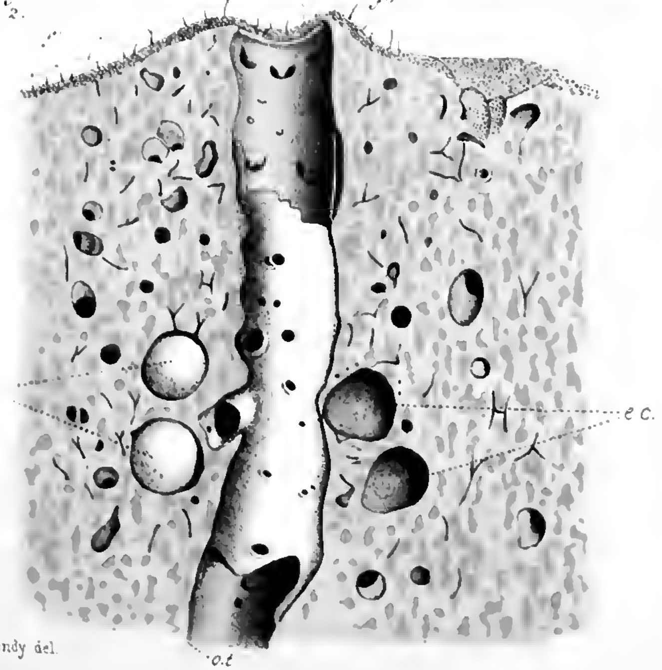

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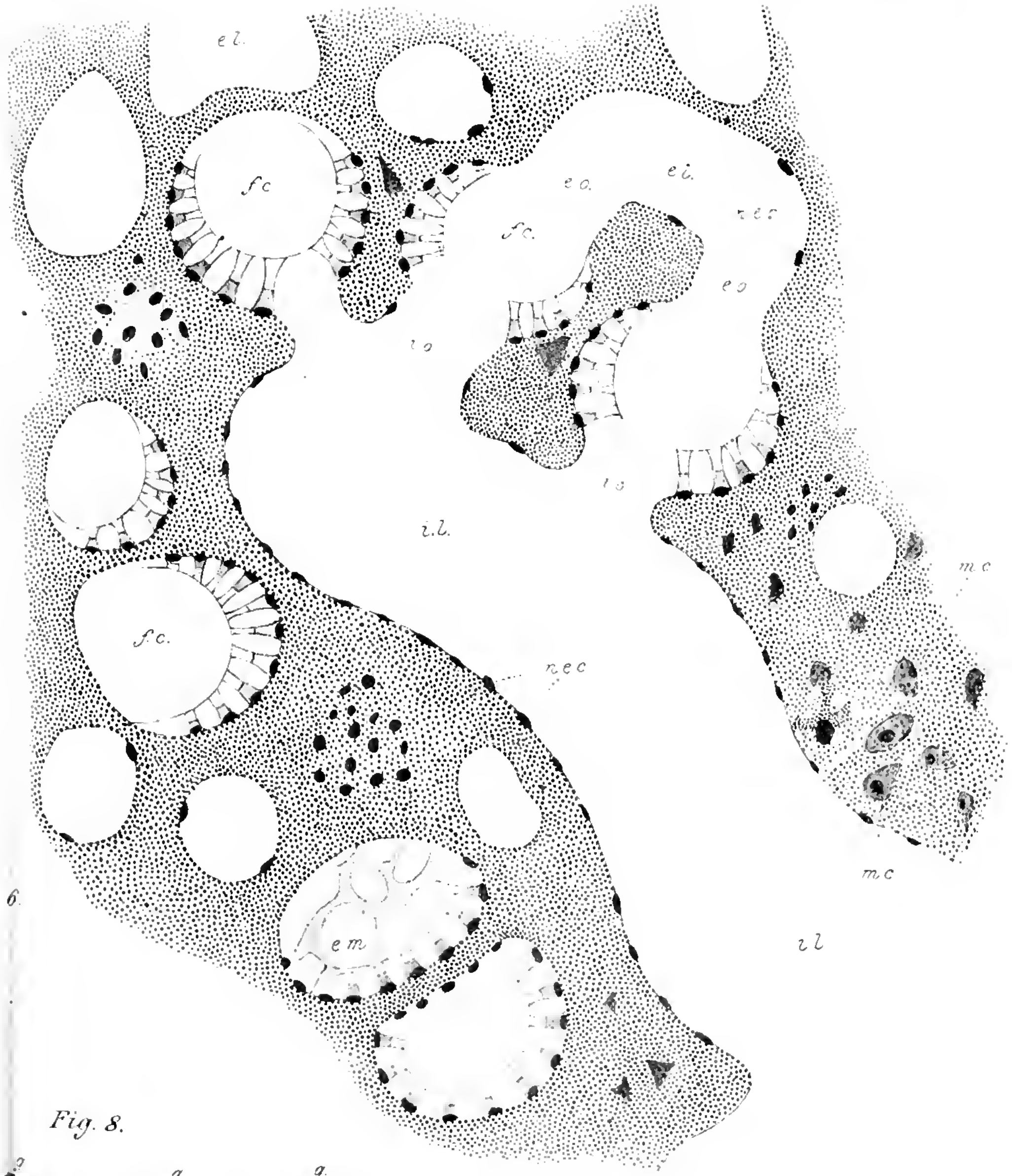
Fig. 6



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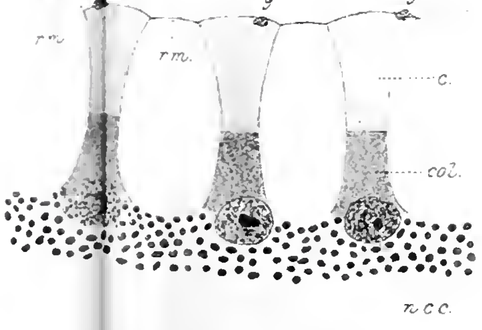

Fig. 7.

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Fig 9

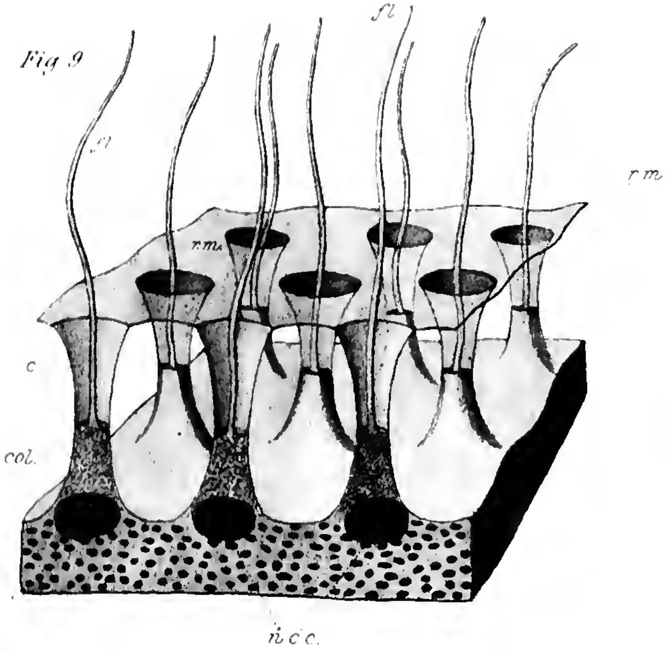
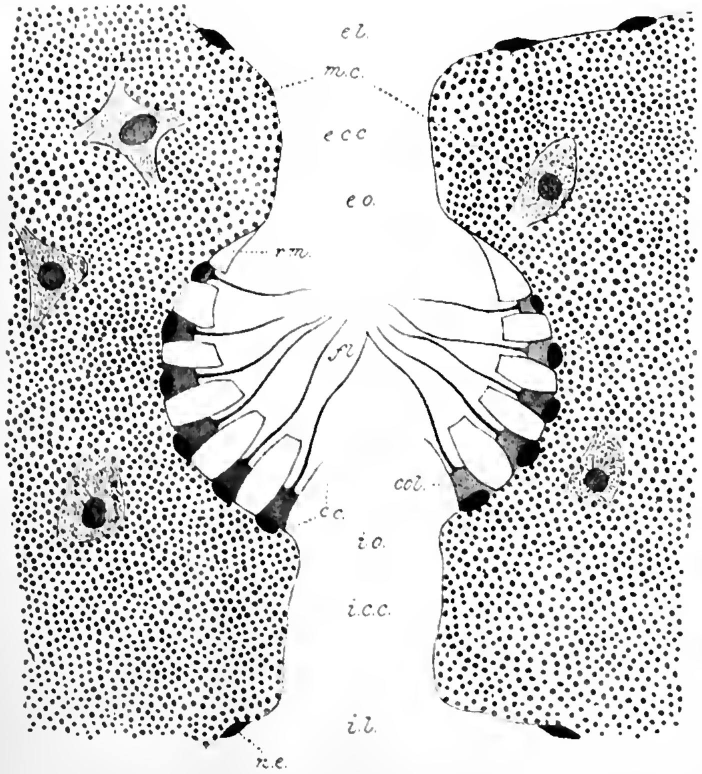


Fig. 10.



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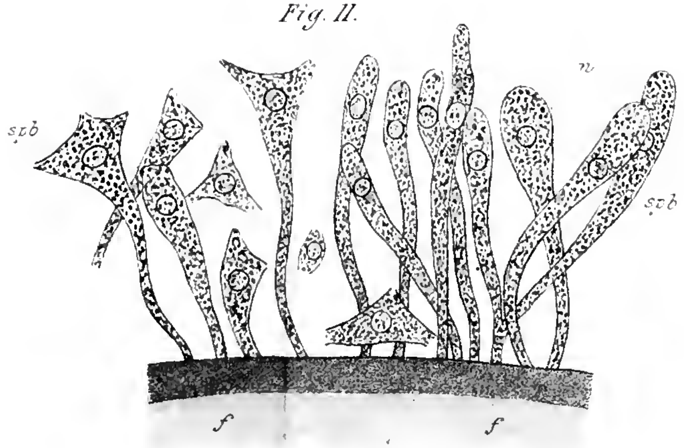

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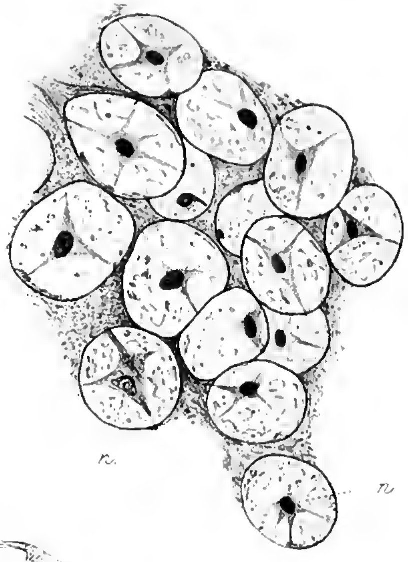

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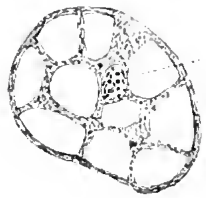

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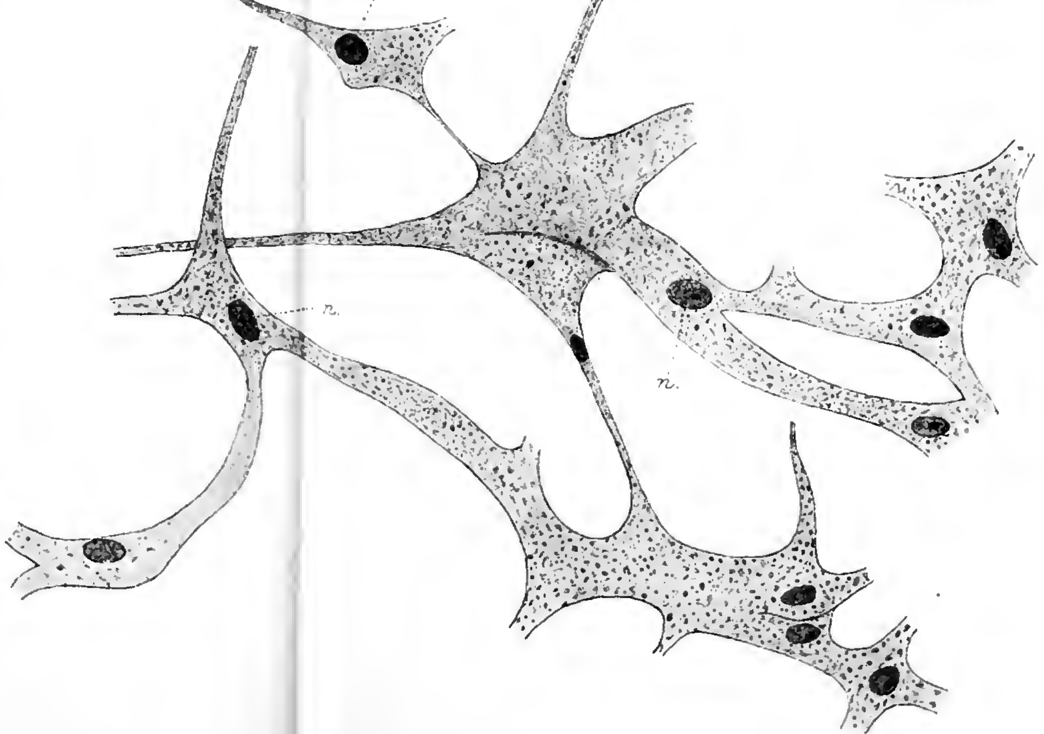

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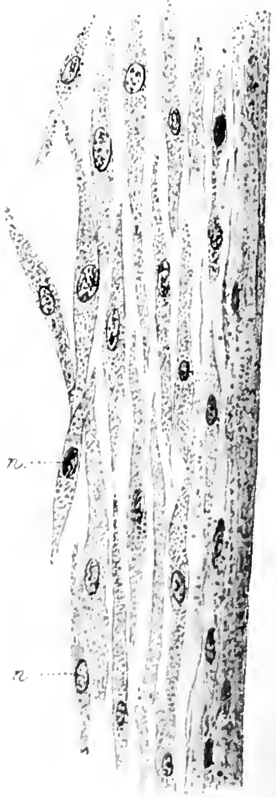

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Fig. 23.

Fig. 16.

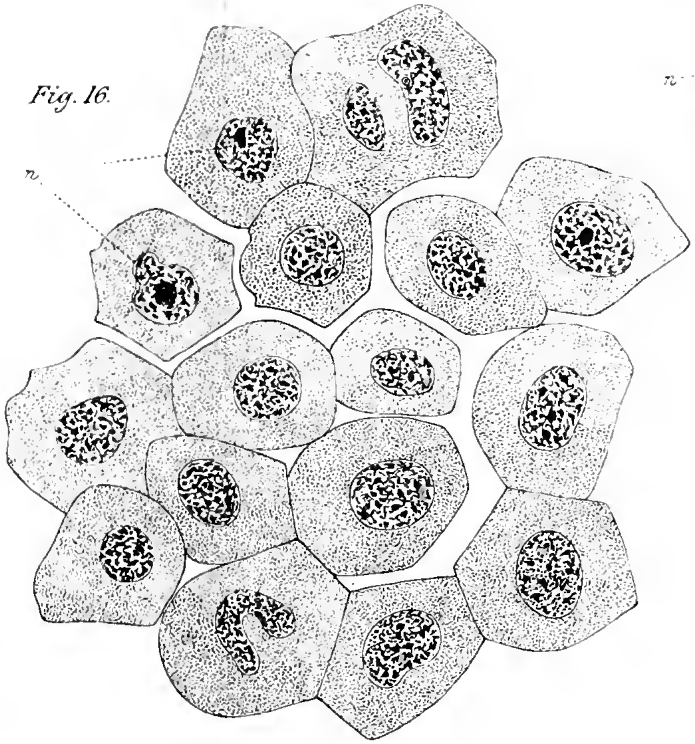


Fig. 22.

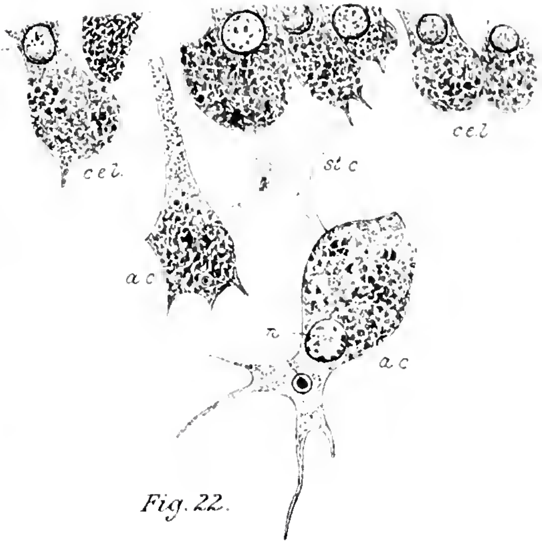


Fig. 17.

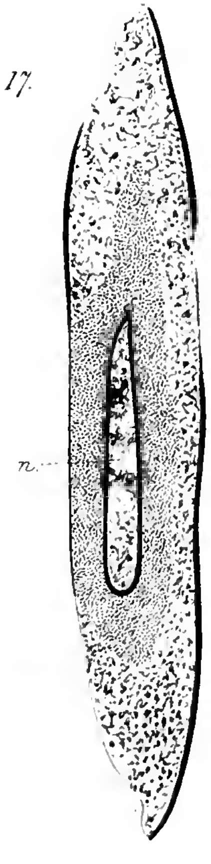
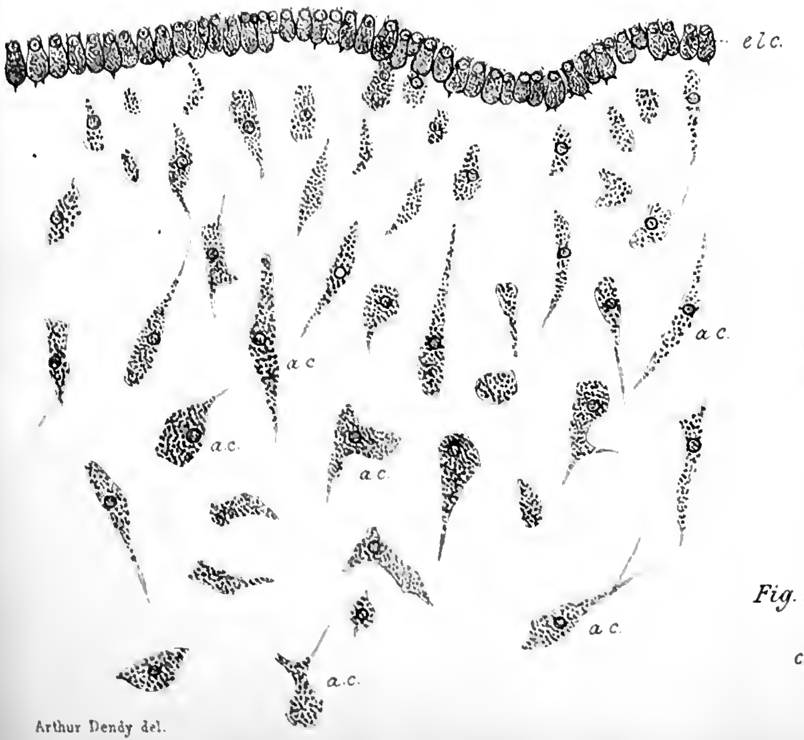


Fig. 19.



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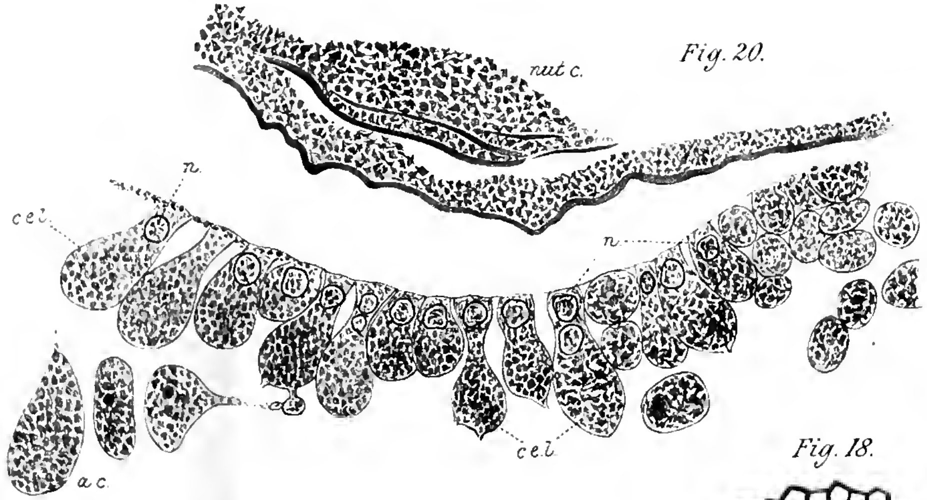


Fig. 18.

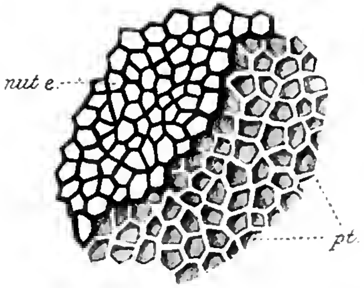
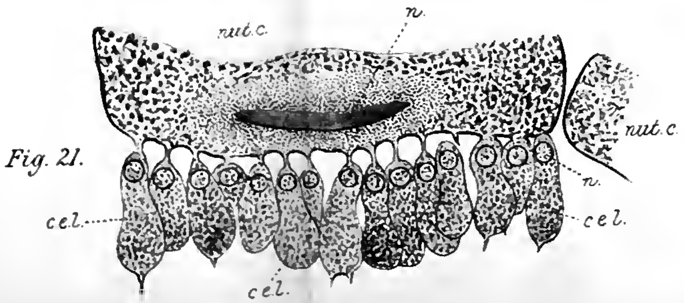


Fig. 21.



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On Some Points in the Natural History of Fungia.

By

J. J. Lister, M.A.

During a visit to the Seychelles Islands at the latter end of last and the beginning of the present year I was so fortunate as to find species of the Madreporian Coral Fungia, both in the fixed and free conditions. Owing to the shortness of the time now at my disposal I have not been able to examine the material I have brought home as completely as I hope to on some future occasion, but as it throws light on some of the stages of the life-history of this group of Corals which have hitherto been obscure, a preliminary account may not be without interest.

The Fungias are abundant in water from one to six feet deep towards the outer edge of the broad fringing reef of Mahé, the principal island of the group. The reef is divided by deep winding channels, whose sides are formed by living Corals of many kinds. Between the channels the Coral comes very near the surface, so near that the summits of the branches of a blue tipped Madrepore, which is very abundant in these shallow areas, are out of water at low tides, though apparently without injury to the Coral.

Over some areas this Madrepore has died, and it was on the dead branches that the fixed stocks of the Fungia were most abundant. Among the free forms Fungia discus and F. dentata were abundant.

The young fixed stocks of Fungia are attached by a broad base, and have vertical thecal walls. The youngest that I found have six septa conspicuously larger than the rest (Fig. 1), one at either end of the long axis, passing through the mouth, and two symmetrically placed on either side. In the intervals smaller septa have made their appearance, but they are lower and do not approach so near the centre as the six large ones. In each interval there is one in the centre and two small ones on either side of it. The appearance of fresh septa does not, however, take place quite regularly, for while in one interval between the primary septa there may be three smaller ones well developed, in another the central one alone may be only just discernible, at least in spirit specimens, in which the skeleton is invested with the soft tissues.

Fig. 1.—A young fixed stock of Fungia (sp.?) × about 25. From a specimen preserved in spirit.

The young stock has, as has been stated, vertical thecal walls. After a certain, apparently very variable, height is attained the upper part begins to widen out, forming at first a very shallow cup with thecal walls facing outwards and downwards, and finally a disc, depressed in the centre, with the thecal walls facing directly downwards. The cup or disc is attached by the narrow stalk, the first formed part of the stock.

After the disc has become distinctly formed, though the breadth it may have attained is very variable, a remarkable process sets in, which results in its separation from the stalk which has hitherto supported it. In a plane at right angles to the axis of the stalk, at a point where the upper part is beginning to widen out, absorption of the calcareous skeleton takes place, which goes on till the disc is connected with the stalk so weakly that a very small force is needed to set it free. It often happens that the disc falls off when the object on which the Fungia is growing is lifted from the water.

When the disc is set free it has a round scar in the middle of the under surface which corresponds with a similar scar at the summit of the stalk. In the scars the following parts of the skeleton are exposed, with the soft tissues investing them. On the outside there is a section of the thecal wall. Passing from this towards the centre are sections of the septa, and these unite with the trabeculæ which fill in the middle. In the disc there is no direct communication with the gastric region, except through the interspaces among the trabeculæ. The surfaces of the calcareous structures where absorption has taken place are white and opaque as compared with the general appearance of the hard parts of the Coral.

The disc thus liberated is carried into some depression in the reef, where it lies unattached, leading an independent existence. The scar on the aboral surface becomes covered in, and though it remains distinguishable for some time, ultimately all trace of it is lost. On the separation of the disc the stalk is left with a truncated top, slightly depressed in the middle.

The first change which takes place that is visible in dry specimens is in the state of the septa (Fig. 2). These, instead of terminating in broken edges, throw up delicate fluted laminæ with serrated edges, which project above the level of the other structures of the scar.

A mouth is formed in the centre, and the lips appear, in spirit specimens at least, to be almost in contact with the trabeculæ below. As the septal laminæ rise higher a thecal wall becomes formed round them, in some places continuous with the thecal wall of the stalk, but generally springing a little within its margin, so that the edge of the old thecal wall remains as a prominent ridge round the stalk. A new cup is thus formed, not as a bud but as a product of the growth of the structures already existing in the base of its predecessor. As its walls grow higher they become more and more expanded outwards, until a new disc is formed supported on a short stalk which springs from the point where the first disc was separated.

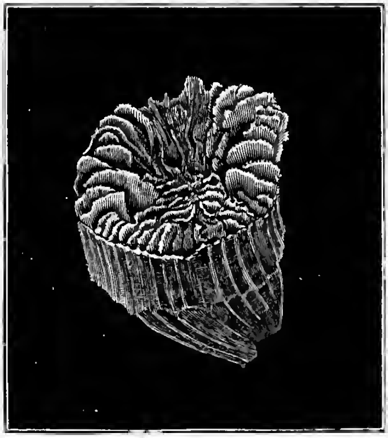

Fig. 2.—A nurse stock of Fungia (sp. ?), from which a disc has been recently separated × 3. The formation of a new disc has begun, as is indicated by the laminæ which have been formed on the edges of the septa in the stalk of the old one. The ridge half way down the Coral indicates the line of separation of an older disc. From a dried specimen.

This second disc in its turn is set free by absorption of the calcareous skeleton at a point where the stalk begins to widen into the disc, and in due course a third disc is formed. As the process is repeated the stalk grows in height step by step, each new disc that is formed being detached at a point above that from which its stalk springs. These successive additions are indicated on the common stalk by ridges which mark the planes where discs have been separated.

The specimens obtained show many instances of the formation of buds at the expanded bases of the fixed stalks, but in none was there any evidence that the disc which grows on the scar at the summit of the stalk is produced by budding. The structures of the new disc are, as we have seen, the product of the growth of the corresponding structures in the stalk of the disc which went before it.

Contributions to the Knowledge of Amphioxus lanceolatus, Yarrell.

By

E. Ray Lankester, M.A., LL.D., F.R.S.,
Professor in University College, London.

With Plates XXXIV, XXXV, XXXVI, XXXVI*A*, & XXXVI*B*.

It is now fourteen years since I published in the 'Quarterly Journal of Microsc. Science' (vol. xv) some notes on the structure of Amphioxus. I have delayed publishing until the present date fuller illustrations of the facts then recorded, but have made use of my material in annually recurring lectures at University College.

One statement made in the notes above referred to I am not able to confirm, and must withdraw. I refer to the supposed confirmation of Johann Müller's statement (1) that there is a pair of apertures on either side of the oral sphincter (velum of Huxley). I stated that these apertures lead from the pharynx to the præoral space. Müller had described them as leading into the metapleural canals. In reality there are no such apertures at all.

The "brown funnels," which were described in my original note, are the most important structures which I have now to illustrate. Curiously enough, they have escaped all subsequent observers with the exception of Mr. William Bateson (2), of St. John's College, Cambridge, who confirmed my observation as to their position and character, and has compared them very significantly with the "collar-pores" of Balanoglossus.

My purpose on the present occasion, in addition to that of definitely exhibiting the position and form of the brown funnels, is (1) to furnish a few numerical data of importance for the anatomical discussion of Amphioxus; (2) to correct some errors which appear to be current as to the existence or non-existence of spaces of one kind and another in the body and gill-bars of Amphioxus; and (3) to submit some drawings which represent, in a semi-diagrammatic form, the structure of Amphioxus, not merely as seen in sections or dissections, with all the imperfections necessarily arising from the action of preservative media, but as reconstructed and corrected from numerous specimens, so as to give as nearly as may be a true conception of the undistorted organism.

External Marks and Numerical Characteristics.

The general outline and form of a living specimen of Amphioxus lanceolatus is given in Pl. XXXIV, fig. 4. The drawing is constructed from sketches made by me at Naples from the living animal, and has been corrected by subsequent study of preserved material. When Amphioxus is alive and at rest the atrial chamber is dilated in such a way that its median ventral surface projects below the two lateral ridges, for which I have proposed the name "metapleura." I doubt whether in life this surface is ever contracted to the extent which it is in even the most carefully preserved specimens, such, for instance, as that shown in Pl. XXXV, fig. 3. That specimen was treated with Kleinenberg's picro-sulphuric solution, followed by increasing strengths of alcohol; and I have not yet found any treatment which gives a less general distortion of the body than this. Specimens placed when living into alcohol assume the most extreme distortion, owing to the violent contraction of the transverse ventral muscle of the atrial wall, and the shrinking of tissues and spaces. Such an extreme contraction is exhibited in the figures of Rolph's important treatise on Amphioxus (3), and to a less extent in figs. 2 and 3 of Pl. XXXIV accompanying this memoir. In Pl. XXXVI I have given a diagram of a transverse section with such form and proportion of all regions and spaces as I have been led to conclude are actually maintained in the living state. I do not know of any one reagent which gives equally good results for all parts of the Amphioxus body. I have found it necessary to study specimens preserved in several different ways.

Grooves of the Ventral Wall.—Even when somewhat distended, as shown in Pl. XXXIV, fig. 3, the ventral wall of the atrium of Amphioxus exhibits longitudinal plaiting. These folds have been observed and counted on living specimens at my request, by my friend Balfour, and by others who have had the opportunity of studying living Amphioxus at Naples, since I was there in 1875. And there is no doubt that they are not "artifacts," but exist in the living state, though their depth is increased by the unnatural contraction caused by preserving fluids. They are best seen in the ventral view of a living specimen given in Pl. XXXIV, fig. 4. As far as I can ascertain they do not vary in number in the same individual, except as the result of the general increase of the animal's size. All the folds do not extend the whole length of the ventral surface: some stop short anteriorly. I have counted from six to eight on each side of the middle line. They entirely disappear when the ventral wall of the atrium is fully stretched, as it is when the generative products are full grown and ready for extrusion (see Pl. XXXV, fig. 4). Their production is accounted for by the insertion of some of the fibres of the ventral transverse muscle into the somewhat thick tegumentary connective tissue, in a series of lines corresponding to the grooves. This insertion can be readily observed in thin transverse sections (see Pl. XXXVI*A*, fig. 2).

Absence of Canals below the Ventral Plaited Integument.—The epidermis supported by a fine basement membrane frequently becomes separated by the action of reagents from the thick subjacent connective tissue of this region, and has given rise to an erroneous conclusion, to the effect that there is a series of ventral canals underlying the plaited epithelium. Or, on the other hand, the muscle becomes separated from the deeper layer of the cutis, and a similar mistake has arisen. This error is made by Stieda (4), Rolph (3), Langerhans (5), and Schneider (6). The true relations are shown in the drawing, Pl. XXXVI *A*, fig. 2.

Number of Myotomes.—The number of myotomes is an important and fundamental numerical character of the species of Amphioxus. In the Amphioxus lanceolatus of Naples there are sixty-one of these myotomes. The last myotome is extremely delicate, and it is by no means easy to count the whole series with certainty. In some large specimens I have counted sixty-two myotomes.[1] Dr. Günther (7) in his important account of the genus Branchiostoma (= Amphioxus) in the 'Report on the Zoological Collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert,"' published by the trustees of the British Museum, 1884, gives sixty as the number of myotomes in specimens of A. lanceolatus of Naples, fifty-nine in one from Polperro, and sixty-one in a specimen from the Scandinavian coast. The number in other species varies as follows:—In A. elongatus from the coast of Peru, 79; in A. bassanus from Bass's Straits, 75 or 76; in A. Belcheri from the coast of Borneo, 64 or 65; in A. caribæus from Rio de Janeiro, 60 or 59; in A. cultellus of Peters, 52.

It appears that the full number of myotomes is acquired by Amphioxus at a very early period in its growth, even before (?) the complete formation of the epipleural chamber. It is not quite certain that the number of myotomes varies in A. lanceolatus from fifty-nine to sixty-two, as would appear from the numbers above given. The discrepancy may be due to the difficulty of accurate counting, and to the recognition or omission of the terminal myotome. The question, therefore, needs some further study.

Position of Mouth, Atriopore and Anus.—The mouth of Amphioxus is that small median aperture surrounded by a well-developed sphincter muscle which is concealed by the oral hood. It is not correct to call the margin of the wide space

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[1] I have a note of the number of myotomes counted in four large specimens besides those referred to in the text, viz. respectively fifty-nine, sixty-two, sixty-one, and sixty-one. In the figure in Plate XXXIV I have given sixty-two myotomes, but sixty-one is the usual number.

bounded by the oral hood "mouth," since the true mouth above indicated exists before the oral hood is formed. The oral hood is the præoral portion of the epipleural folds, which post-orally give rise to the "atrial," "branchial," or "epipleural" chamber. The true mouth is that which has been compared by Huxley (9), whose nomenclature is followed by Langerhans, to the velum palati of Cyclostome fishes. It has twelve delicate tentacles projecting freely from its margin backwards into the pharynx. The grouping of these has not hitherto been satisfactorily figured in any account of Amphioxus; they are represented in Pl. XXXVI*B*, fig. 12. They were seen by Rathke (8) and by Joh. Müller (1), who figure them as seen when the sphincter is slit open; their minute structure is figured and described by Langerhans, who calls them papillæ.

It is difficult to assign a position in relation to the myotomes to those organs which lie more ventrally than the segmented musculature of the body wall. The myotomes are separated from one another by connective-tissue septa, each of which, instead of being vertical, is directed obliquely upwards and backwards in the dorsal half, and obliquely downwards and backwards in the ventral half, of its extent; and as the myotome becomes very narrow and almost horizontal before it disappears ventrally, it is not possible to assert with any assurance that structures lying below the region into which the myotomes extend are behind or in front of any given one of these obliquely directed structures.

I am inclined to the view that the oral sphincter is morphologically in front of the first myotome, though its position coincides approximately with a vertical line drawn through the anterior angle of the seventh. This back-pushed position of the ventrally placed organs in relation to the myotomes of the body wall is characteristic of Amphioxus, and is connected with the establishment of an independent metamerism of the alimentary canal, which, after the early larval condition, seems to be in no definite relation to the metamerism of the body wall.

The atriopore or ventral median aperture of the peripharyngeal chamber formed by the down-growth and fusion of the epipleural or opercular folds, is so placed that it is possible, by carefully tracing back the obliquely directed myotomes, to arrive at a definite conclusion as to its position. It appears to me to coincide with the 36th myotome, whilst a vertical line drawn from the anterior angle of the 41st myotome passes through its posterior margin.

The anus coincides with the septum separating the 51st from the 52nd myotome, and I count ten post-anal myotomes. The series of numbers thus arrived at may be written thus: 36+15+10=61.[1] Dr. Günther gives four different enumerations of the myotomes of specimens of Amphioxus lanceolatus from different localities, none of which are precisely the same as that which I am inclined to regard as characteristic for Neapolitan specimens, viz. 35+12+12=59 (Polperro); 36+14+11=61 (Scandinavia); 34+13+13=60 (Naples); 35+12+13=60 (Naples).

The Number of the Fin-Rays.—Amphioxus is provided with a continuous dorsal fin which reaches anteriorly below the extreme terminal portion of the notochord and becomes continuous with one side of the præoral hood, viz. the the right. Posteriorly the fin-like expanse is continued round the notochord and runs forward on the ventral surface along the median line, lying, however, to the right of the anus. Coincidently with the last twelve myotomes the fin is expanded both in its dorsal and ventral regions so as to form a lozenge-shaped caudal fin. It runs forward on the ventral median line as far as the atriopore. The base of the fin is supported by a series of fin rays which are short cylindrical pieces of a kind of connective tissue. The dorsal fin-rays are in a single series;[2] those on the ventral surface between anus and atrio-

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[1] I have also notes of countings of Naples specimens which give 35 + 14 + 13 = 62; 35 + 14 + 12 = 61; 35 + 16 + 10 = 61; 36 + 15 + 11 = 62.

[2] The very first fin-ray of the dorsal series is bifid at its base, as shown in Pl. XXXVI*B*, fig. 11, tending to show that the ventral series are not so peculiar in their double character as is suggested in the text.

pore form a double or paired series. A very peculiar fact with regard to these fin-rays is that whilst each is connected at its base with a strong ridge of connective tissue which forms a continuous median plate, springing from the roof of the skeletal neural sheath, yet on all its other faces each fin-ray is free, lying in a lymph space. The lymph space surrounding the fin rays is not a continuous tube but is divided into compartments one to each fin-ray ; and each compartment is lined with a pavement of endothelial cells which is extended over both the wall of the compartment and the free surface of the fin-ray. The liquid in the compartment separating the fin-ray from the wall of the compartment is coagulable. The nuclei of the cells on the free surfaces of compartment and fin-ray may be readily observed in well-stained sections. It appears that the compartments filled with lymph are antecedent structures to the fin-ray which eventually comes to occupy a large part of the space, since in both the anterior and the posterior regions of the dorsal fin the fin-rays are relatively small and occupy but little of the lymph-space, whilst at the extremities of the series the fin-rays actually disappear entirely, leaving only the lymph-holding compartment to represent the whole structure. Anteriorly, the fin-ray lymph-space extends as far forward in the form of a fine canal as the notochord itself, and is divided into five or six compartments devoid of solid rays. Posteriorly I have not ascertained its precise termination, but there are several compartments overlying the last six myotomes which in adult specimens are devoid of fin rays. I think that the number of compartments both anteriorly and posteriorly not occupied by fin-rays is larger in half-grown than in fully-grown specimens, and that the volume and solidity of all the fin-rays is greater in the more fully-grown individuals. Anteriorly, the fin-rays do not commence until, in proceeding from before backwards, we have passed that region of the nerve-cord which is in relation with the olfactory pit. The figure given by de Quatrefages (**10**) of this region, being a careful drawing from a living specimen, shows excellently the condition of the first few fin-ray spaces and the first rays. I have not thought it desirable to reproduce that figure in the present memoir nor to produce one like it, but the reader is referred to the French naturalist's drawing as one giving valuable data. An extremely important fact with regard to the fin-rays of the dorsal series is that they are between four and five times as numerous as the myotomes, and the question arises whether they have any definite numerical relation to the myotomes. I have counted from 250 to 260 fin-rays in an adult Amphioxus lanceolatus with sixty-one myotomes, no rays being developed over the last six. Supposing we exclude the imperfectly developed anterior and posterior regions, we find that there are very nearly 220 fin-rays for forty-five myotomes, approximately a relation of five to one. But I am unable to accept the view that there is any real relation between the metamerism of the fin-rays and the metamerism of the myotomes. The fact that anteriorly there are less than five fin-rays to a myotome, viz. four, and posteriorly more than five, is opposed to such a relationship, whilst further, the numerical features of the paired ventral fin-rays are entirely destructive of any theory of the kind, for we find in the ventral series (on an average) thirty-four pairs of fin-rays to twelve myotomes.

The paired fin-rays of the ventral post-atrioporal mid-line are, like those of the dorsal series, contained in a series of compartments, which are divisions of a lymph-space. The space is not divided into a right and left half, but is simple. This lymph-space is continued as a contracted canal with coagulable contents along the mid-line posterior to the anus for the space of several myotomes. I am not able to say precisely where it terminates. A reinvestigation of the tail by transverse sections would at once settle this point.[1] The number of the paired fin-rays varies a little. There are

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[1] Anteriorly the dorsal fin-ray lymph-space ends with the notochord as a very contracted canal overlying it. It is of some importance to note that in this extreme anterior region there is a ventral lymph-space below the notochord of the same nature as that above it, but devoid of fin-rays, though divided into compartments, six in number. (See Pl. XXXVI*A*, fig. 3, and de Quatrefages.)

fifteen myotomes between the atriopore and the anus, and the double fin-rays become exceedingly small and terminate before the anus is reached. In three specimens counted they were developed in relation to the first twelve of the fifteen myotomes between atriopore and anus; in one there were thirty-four paired rays, in the second thirty-nine, and in a fourth forty-one.

It is not improbable that the double series of ventral fin-rays represent a posterior continuation of the same primitive lateral fold on each side of the body, which in the anterior two thirds of its extent becomes sufficiently large to wrap round the ventral surface of the body, and by fusion with its fellow along the mid-line to form the atrial chamber, whilst posteriorly its line of offgrowth has descended on either side, so as to lead to an approximation and ultimate fusion in the mid-ventral line, forming the double ventral fin. It is of significance in this connection that the paired structure of the ventral fin does not extend beyond the anus, and that the azygos fin is continued ventrally to the right of the anus, whilst anteriorly there is a continuity of one lateral fold (the right half of the præoral epipleur or hood) with the dorsal azygos fin. This continuity would be similar to that of the azygos fin (passing to the right of the anus) with the series of paired ventral fins, if the view should be established that the paired fins are the conjoined post-atrioporal extensions of the epipleural folds.

It is important in this matter to distinguish the metapleural canals and cartilages from the epipleura upon which they develop (see Pl. XXXIV, figs. 4 and 5). The metapleura, as shown in the figures just cited, are continued posteriorly beyond the atriopore and beyond the first two pairs of ventral fin-rays. This is evidence in favour of the view that the paired ventral fin-rays are continuations of the paired epipleura, for in front of the atriopore the area between the two metapleura is formed by the fusion of the two epipleura, and it is a legitimate inference that behind the atriopore what lies between the two metapleura is also formed by fused epipleura.

The Number of the Gonad Pouches.—The cœlomic sacs in which the reproductive cells develop are twenty-six in number on each side of the body, and correspond to twenty-six of the myotomes.[1] On account of the oblique shape of the myotomes it is not easy to decide precisely which of the thirty-six myotomes between the anterior snout and the atriopore are those to which the gonad pouches correspond. I am of opinion that the last gonad pouch corresponds to the last præ-atrioporal myotome, and this would make the first coincident with myotome No. 10, and the last with myotome No. 35.

The important fact is that the gonads are affected by the same metamerism as that which affects the musculature.

Occasionally specimens of Amphioxus occur in which the anterior one or two or the posterior gonad pouches are not developed, whilst the others are in full ripeness; and in specimens taken in the autumn the entire series of gonad pouches are usually in an extremely rudimentary condition.

Number of the Præoral Tentacles.—The circular group of pinnate tentacles to which Amphioxus owes its earlier name of Branchiostoma, presents great numerical variations. The tentacles increase in number as the Amphioxus increases in size. Their first appearance is not known, but I have records of small individuals with twenty, of middle-sized with thirty, and of large individuals with forty tentacles. I am indebted to Dr. Hugo Eisig for kindly counting specimens of various sizes for me at Naples.

The addition of new tentacles appears to take place at the middle point of the ventral side of the ring-like margin of the præoral hood, and they are formed in pairs, right and left, the last formed being exceedingly small. There is no median tentacle, either dorsal or ventral.

The Number of the Pharyngeal Gill-slits.—It seems from the descriptions given by Kowalewsky (**11**) that the gill-slits which first appear in the larva are in definite relation to the

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[1] In some specimens I have counted twenty-seven, and in some twenty-nine; in others again only twenty gonad pouches on one side, whilst twenty-six are present on the other side.

myotomes, but that this relation is not subsequently maintained.

The accounts of the late larval condition of Amphioxus are not sufficiently satisfactory to enable us to formulate a very definite conclusion as to this early relation of the gill-slits to the myotomes. It is, however, quite certain that after the larval phase all relation between the number of the myotomes and the number of the gill-slits is lost. The gill-slits go on increasing in number by addition at the posterior end of the series throughout the period of growth—probably as long as the animal lives—whilst the full number of myotomes is acquired at a very early period, and is not subsequently increased. Owing to this fact it is possible in any Amphioxus to observe the mode of formation of the gill-slits, and it is found that they originate as oval or nearly circular perforations of the proper body wall, which become divided each into two by the growth from the dorsal margin of the oval slit of a longitudinal bar or tongue, comparable to the tongue of a Jew's-harp, which thus divides each primary slit or gill aperture into two.

The tongue bars can be distinguished throughout the series by the fact that they are supported by a hollow chitinous rod, whilst the adjacent bars separating primary slits from one another are solid (Pl. XXXVI*B*, figs. 1 and 2). Also the primary bars are provided with a plate-like projection on their external border which becomes deeper dorsalwards and shallower ventralwards. This plate-like projection is soft-walled and hollow, containing a space which communicates with the "dorsal" or supra-pharyngeal cœlom. In my earlier paper (**12**) I called these soft plate-like projections the pharyngo-pleural folds. In the more dorsal or upper part of the bars the pharyngo-pleural folds are so deep as to rest for some distance against the inner face of the down-grown epipleura. In consequence of the oblique and almost horizontal position of the bars and slits throughout the middle third of the perforate region of the body, and, in consequence of the adhesion of the pharyngo-pleural folds to the epipleura, the atrial chamber is divided, for a part of its extent, into a number of nearly horizontal passages which may be compared to the series of parallel adherent tube-like passages connecting the gill pouches of Myxine with the branchial pore of that animal. When the development of Myxine can be studied, I should be anxious to inquire whether the tube-like passages in question are formed by the septation of a primitively simple subopercular cavity through the outgrowth of interbranchial septa as in Amphioxus.

The number of gill-slits, counting each of the primary slits as two, observed by Johann Müller in a small transparent specimen, was 50, in individuals of an inch long 80 to 100. In individuals a little over an inch in length I have counted 96 slits, and in larger specimens (nearly two inches long), 124. To arrive at the number of primary slits we have to halve these figures, since each pair of slits is formed in the way above noted.

The independence of the gill-slits in relation to the metamerism of the body wall is related to the following facts. (1) The myotomes increase in volume during growth but not in number. (2) The whole pharyngeal region of the body increases in volume during growth, and the point at which the perforations cease, though it remains throughout life (after a size of three quarters of an inch has been reached) in approximately the same relative position to the superjacent myotomes, viz. coincident with a vertical line drawn through the anterior angle of the myotomes 27 to 29, yet advances gradually backwards from the former to the latter as growth goes on. (3) The pharyngeal slits do not increase in width, and the increase of the pharynx is made by new local growth at its posterior end. Accordingly new slits are formed in the new-growing region of the pharynx. It thus results that organs which are fixed in position in relation to a particular myotome—for instance, the "atrio-cœlomic funnels," to be described below, of which I have spoken in my earlier paper as "the brown canals," are found to vary in their relative position to the perforated region of the pharynx. In small specimens the atrio-cœlomic funnels are in the same plane with the non-perforated termination of the pharynx; in larger specimens they are seen in sections coincidently with a full series of bars and slits as in Plate XXXVI.

The independent metamerism of the body wall on the one hand, and the gill-slits on the other in Amphioxus, is a matter of some interest in relation to the metamerism of musculo-skeletal axis and branchial bars in craniate Vertebrata.

The Spaces Enclosed in the Body of Amphioxus.—There are three distinct kinds of spaces containing liquid in the living state, which are to be met with in the study of transverse sections of Amphioxus. These are: (1) the atrial cavity; (2) the enteric cavity; (3) hæmo-lymph cavities. The last group is divided into several sections which are more or less distinct from one another; they are (*a*) the vascular system, which, as shown by Schneider, is in open continuity with (*b*) the supra-pharyngeal and perienteric portions of the cœlom; (*c*) the perivascular spaces of the dorsal aortæ; (*d*) the perigonadial cœlom; (*e*) the right and left metapleural lymph-spaces; (*f*) the lymph-spaces of the dorsal and ventral fin-rays; (*g*) the superior and inferior intra-notochordal lymph canals; (*h*) the neuraxial canal; (*i*) the myocœlomic pouches or intra-muscular lymph-spaces of the head; (*k*) the series of intra-skeletal lymph-spaces of the myotomes.

As has been mentioned above, it is extremely difficult to arrive at a correct conclusion as to the existence of spaces within the body of Amphioxus, owing to the distorting action of the reagents used for hardening specimens before cutting sections. The chief errors which have been made by previous writers—some falling into one mistake and some into another—are the ascription to Amphioxus of a single wide ventral sub-epidermic lymph canal, or of a series of such canals beneath the plaited ventral region of the branchial chamber, the denial of the existence of natural canals in the metapleura, the overlooking of the intra-notochordal lymph channels, and the assertion of a canalicular communication ("godets" of Moreau) between the contents of the notochordal sheath and the space enclosed by the superjacent, neuro skeletal tube.

The structure of the pharyngeal bars, and the number and character of the spaces contained in them, as shown in transverse section, also have been the subject of divergent and erroneous statements.

The atrial cavity can be readily traced in sections of well-grown specimens, owing to the fact that the epiblastic epithelium by which it is lined, is loaded very often with brown pigment granules. For the purpose of tracing the atrial cavity, a specimen should be chosen which has the brown pigment well developed; it is more abundant in some individuals than in others. The general limitation of the atrial cavity as seen in a transverse section about the twenty-seventh myotome, is shown in the diagrammatic figure given in Pl. XXXVI. Other facts with regard to the atrial cavity are shown in the "reconstructed" dissection of Pl. XXXIV, fig. 1.

A curious fact with regard to the atrium (first described by Rolph) is the existence of a cæcal prolongation of its cavity beyond the atriopore posteriorly. This atrial cæcum pushes its way as a tapering blind sac into the perienteric cœlomic space behind the atriopore, and occupies a position between the intestine and the musculature of the body wall. It reaches as far back as the anus, where it terminates blindly. It is represented in Pl. XXXIV, fig. 1, for the first time as exposed in a simple dissection, Rolph's and Langerhans' figures showing it in transverse section.

The enteric cavity of Amphioxus presents three main regions, viz. the pharynx, the intestine, and the cæcum. Owing to the enclosure of the true original surface of a large part of the body by the atrial or epipleural folds, a misleading nomenclature is apt to be applied to the regions of the body thus enclosed; we are led to overlook the fact that the wall of the perforated pharyngeal region, the wall of the cæcal region, and the wall of the intestinal region as far as the atriopore, are not the proper walls of pharynx, cæcum, and intestine, but in reality epidermis-clothed somatopleur or body wall, enclosing within it more or less complete cœlomic space, and the portion of alimentary tract to which the body wall so closely moulds itself. The relation of these parts is shown in Pl. XXXIV, fig. 1, and it is clear enough that we cannot in the præ-atrioporal region separate the various parts of the enteric canal from the closely adherent body wall. The cæcum appears not to be enclosed in a portion of body wall common to it and the pharynx; but there is actually a complete diverticulum of the body wall covering, and fitted to, the cæcum, leaving a small cœlomic space between the somatic and splanchnic elements, as shown in Pl. XXXVI.

I do not propose to enter on the present occasion into detail with regard to the structure of the successive regions of the pharynx, but I may point out that whilst in the anterior region it is broad and heart shaped, in section it becomes posteriorly greatly compressed, as shown in Pl. XXXVI. This shape appears to me to be the natural shape during life; when the gonads are enlarged the pharynx is necessarily compressed throughout that region where it is accompanied by the cæcum.

The numerical relation of the cæcum appears to be as follows:—It is given off as a diverticulum on the right side of the body about the 28th or 29th myotome, and reaches as far forward as the 15th or 14th myotome. These figures apply to adult specimens.

The **vascular system** of Amphioxus appears to be in a condition of degeneration, since it presents a certain limited development of vascular trunks, which do not appear to have a physiological significance in their present relations.

I am not in a position to give a critical account of the vascular system, but it is necessary to draw attention very emphatically to the continuity of the vascular trunks and lymphatic spaces of Amphioxus and their contents, which make it impossible to decide with certainty in all cases whether a given space with coagulable liquid contents is to be considered as blood-vessel or lymph-vessel. Such a communication is described by Schneider and figured by him, showing the free connection of the veins of the cæcum with the dorso-pharyngeal cœlom. Such a communication is suggested by Langerhans in his description of the capillary network on the cæcum. I am inclined to think that there are not distinct capillaries and cœlomic space around the cæcum, but that the space is capillariform.

Some main trunks of the vascular system of Amphioxus are obvious enough in sections. The difficulty is to make out definitely their connections. We have (1) the cardiac or endostylar aorta, a highly contractile vessel lying in the wide cœlomic space below the hypobranchial ridge or endostyle of the pharynx. Anteriorly this vessel dilates into the "heart" of Langerhans, placed just below the sphincter oris. From this "heart" are given off anteriorly a right and left vessel to the oral tentacles, and laterally a single right so-called "aortic arch," a large sinuous vessel, which runs forward and upwards in the right præoral epipleur (right side of oral hood), until it reaches the level of the notochord, where it joins (according to Langerhans) the right "dorsal aorta." This sinuous aortic arch has been described by Rolph as a gland, and in fact it appears to occupy the space in which a glandular structure is developed in the larva.

The dorsal aortæ are two vessels, right and left, underlying the notochordal sheath, and placed on either side of the hyperbranchial groove (see Pl. XXXVI). They extend throughout the length of the perforated pharynx, but unite to form a single "posterior aorta" at the point where the alimentary canal narrows and becomes intestine. This single median vessel can be traced on the dorsal surface of the intestine as far as the anus, beyond which point it appears to be continued as a canal in the ventral part of the sheath of the notochord, finally ending blindly near the extremity of that organ. Similarly in the anterior region of the body the left aorta is continued forward in front of the mouth as a narrow canal in the left side of the notochordal sheath, and finally, I am inclined to think, opens into the cavity of one of the cephalic myotomes, the cavitary structure of the mesoblastic somites surviving from the embryonic condition in this region. The right dorsal aorta is said by Langerhans to communicate with the right aortic arch, but I doubt this. I am not very certain on the point, but I think that it ends blindly. Its place is taken in the præoral region by a branch given off from the "aortic arch," which runs forward in the substance of the notochordal sheath on the right side, parallel with the forward continuation of the left aorta, and these two vessels undoubtedly communicate beneath the notochord by a transverse channel. Finally, the right-side vessel, like that of the left, appears to communicate with the cœlomic cavities of the anterior myotomes.

Schneider has described a series of lateral vessels given off from the dorsal aortæ and running into the primary and secondary (or tongue-like) bars of the pharynx, through which they are supposed to communicate with the cardiac endostylar vessel. I have not been able to trace these lateral branchial vessels in transverse sections, though I have traced a branch from the endostylar vessels into each primary bar (see Pl. XXXVI*B*, figs. 4 to 9).

Upon the inner face of the epipleura below the atrial tunic a blood-vessel has been described by W. Müller (13), running longitudinally. The vessel is seen especially in specimens where the gonad pouches are rudimentary and is related to their development. It furnishes capillaries to the testes, but the connection between it and other blood-vessels has not been observed.

Upon the wall of the intestine and upon the wall of the cæcum there are blood-vessels. Those on the intestine are large and more numerous in its posterior region. They gather together anteriorly and are continued into the endostylar or cardiac subpharyngeal trunk, where the alimentary tract enlarges to form the pharynx. The vessels on the cæcum form a network which has been described by Langerhans. They give rise to a network of capillaries, and together with the capillaries described by the same author in the testes, are the only capillaries present (so far as my own conclusions go) in Amphioxus. The vessels of the cæcum communicate, according to Schneider, with the dorso-pharyngeal cœlom at the anterior extremity of the cæcum through the cœlomic spaces within the pharyngo-pleural pouches of the primary bars of the pharynx, which rest against and open into the blood-holding cavity which surrounds the cœlom. I can confirm this observation from the study of transverse sections made by my pupil, Mr. Willey.

The question as to how the blood which is brought by veins into the cardiac aorta or great contractile blood-channel underlying the hypopharyngeal ridge "circulates," or whether, indeed, it circulates at all, has not been, in my judgment, satisfactorily answered, and renewed investigations are needed. This is in part due to the difficulty of investigating the structure of the pharyngeal bars and of arriving at a certain conclusion as to what are real natural spaces and channels and what are artifacts.

The structure of the pharyngeal bars is shown in Pl. XXXVI *B*, figs. 1 and 2, which represent sections at right angles to the length of the bars. As is well known, from the observations of Müller and others, the bars are not all similar, but of two kinds, viz. (1) those which correspond to the division between primary gill-slits, the "primary bars," and (2) those which form by a growth downwards from the dorsal margin of a primary slit, dividing it into two secondary slits. These are in relation like the tongue of a Jew's-harp, and may be called "tongue-bars." The development of these bars may be seen in any Amphioxus continually in progress in the posterior region of the pharynx. The chitin-like material which forms the skeleton of the pharynx is deposited in the form of rod-like tracts beneath the epithelium (in the cutis-layer) bounding the margin of the gill-slits. Accordingly there is a double rod in each primary bar, one half corresponding to each of the adjacent gill-slits. At each end of the gill-slit this double rod bifurcates, and each half of the fork runs parallel with the arch-like boundary of the gill-slit, tending to meet the furcal half of the next double rod at the summit of the arch. On the other hand, the rod of the tongue-bar is not of a bifid or double character, but is a single hollow rod, which is continued directly from the mid-point of the upper chitinous arch. It does not at the lower end of the primary gill-slit come into contact with the chitinous lower arch, but simply joins the endostyle or median inferior area of the pharynx, the chitinous material ceasing at the point of junction. The general arrangement of the bars is shown in Müller's original plates, and is so well known that I have not thought it necessary to figure it here.

The primary bars and the tongue-bars differ in other respects besides the fact that the rod of the primary bar is essentially bifid and that of the tongue-bar a hollow single rod. A. Schneider and Langerhans have described the structure of these bars as seen in transverse sections; but I think that the former has erred in assigning too many vascular passages to the bars, whilst the latter has assigned too few. My own conclusions are exhibited in the drawings given in Pl. XXXVI *B*, figs. 1 and 2.

Both bars are flattened like a lath, and are set with the narrowest diameter parallel to the long axis of the Amphioxus. The atrial surface of the bars is clothed with the atrial epithelium (*atr. ep.*), the cells of which are especially deep and large, whilst the brown pigment is limited to a strongly-marked group of cells on each side (*pig.*). The inner face of the bars—that turned towards the lumen of the pharynx—is provided with a peculiar epithelium arranged in three rows (*al.*, *am.*, *ar.*), the cells of which are very narrow and long, with elongate deeply-staining nuclei. These cells resemble those found in group *al.* and *ar.* of the endostylar epithelium (see fig. 9, Pl. XXXVI *B*), and like them carry short cilia. The adjacent sides of the bars bounding the passage between neighbouring bars are lined with columnar cells, which carry very long cilia (*col.*). Below the outlines of these columnar cells an immense number of closely aggregated nuclei, which stain strongly with either hæmatoxylin or carmine, are observed. The superficial series of these (*n.*) probably belong to the columnar cells. Whether the deeper nuclei (*n′.*) are all to be reckoned to epithelium seems doubtful. A clear median space or line exists (*sept.*) which must consist of a connective tissue, and the deepest nuclei would in all probability be referable to that tissue (and therefore to mesoblast).

The chitin-like rod lies near the atrial border of the primary bar (Pl. XXXVI *B,* fig. 1 *Rod*), and similarly in the tongue-bar (fig. 2 *Rod*). In both the rod is grooved on its inner (pharyngeal) face, so as to form a small channel, which is probably occupied by a blood-vessel marked *Bl. vess.* in the figures. This is the only space which I can find in the transverse section of the bars, excepting the larger space marked *cœlom* in the figures, and the fissure more or less complete of the double rod of the primary bars (*fiss.* in the figures), and an occasional (by no means constant) minute defect in the rod of the tongue-bar (*x.* in the figures). The blood-vessels which are given off right and left from the great artery of the endostyle (see figs. 4 to 9, Pl. XXXVI *B*) pass into the bases of the primary bars, where their rods bifurcate, and are possibly and probably continued up the primary bars in the channel marked *Bl. vess.* in fig. 1. It is, however, to be noted that this channel is very narrow relatively to the vessels given off from the median ventral artery of the endostyle, and that the tongue-bars certainly receive no such branches from the endostylar artery, although the channel exists in them also. Schneider figures a vessel passing from the dorsal end of each bar—both tongue-bars and primary bars—into the dorsal aorta; and possibly a communication exists between the vessel of each primary bar and that of the adjacent tongue-bars by means of the transverse junctions which occur at intervals along the length of the bars. I have not been able to satisfy myself as to the existence of the communications with the dorsal aorta described by Schneider, nor as to the existence of vessels in the transverse junctions. At the same time it seems very probable that both exist, and a little further investigation may enable us to recognise them in sections.

Between the chitinous rod and the atrial epithelium of the primary bar is a large space lined by an epithelium (*cœl. ep.*). This is the cœlom, and is in free communication dorsally with the pharyngo-dorsal cœlom, and ventrally with the cœlom of the endostyle. The space becomes deeper and its walls longer as we ascend the primary bar, until it opens as a narrow but greatly extended space into the pharyngo-dorsal cœlom. It is the raised-up walls of this space which form the pharyngo-pleural folds or cœlomic pouches of the primary bars (see Pl. XXXVI).

In the tongue-bars there seems at first sight to be nothing which corresponds to the great cœlomic channel of the primary bars. But when we trace the connection of the tongue-bars with the endostylar tract by means of transverse sections, we find that the canal within the rod which distinguishes the rod of the tongue-bar from the rod of the primary bar is in free communication with the endostylar cœlom (figs. 6, 7, 8, Pl. XXXVI *B*). The canal within the hollow rod of the tongue-bar probably opens dorsally into the pharyngo-dorsal cœlom, although the proof of this by means of transverse sections remains to be obtained by future inquiry.

Variations in the amount and position of the chitinous deposit forming the rods of the pharyngeal bars are frequently found; some of these are drawn in fig. 3, Pl. XXXVI *B*. The most noticeable is the tendency to form a complete chitinous deposit embracing the supposed blood-vessels (*Bl. vess.* of figs. 1, 2, 3), and this may be either fused with the chitinous rod or detached from it as a separate piece. The bifid character of the rod of the primary bars is more obvious towards its extremities where it bifurcates (fig. 3, *h*).

A comparison of the structure of the gill-bars of Amphioxus with the gill-filaments of the Lamellibranchs is instructive, and the latter may throw some light on the former. It can scarcely be maintained that the disposition of the blood-vessels in Amphioxus lends itself to the conclusion that we have here a highly efficient branchial respiratory apparatus. When the existence of extensive communications between the large cœlomic spaces of Amphioxus and its blood-vessels are borne in mind, it becomes probable that the branchial apparatus as we see it is modified as compared with an earlier condition in which the blood-vessels played a more prominent part, and were more largely and distinctly developed throughout the organism. The probably degenerate condition of the vascular system in Amphioxus has led me to doubt whether the spaces marked *Bl. vess.* in figs. 1 and 2, Pl. XXXVI*B*, are really continued as distinct vessels to the dorsal aortæ; it is not unlikely that such a continuation exists, but it is also not unlikely that the original branchial vessels have effected a communication with the cœlom. The generalisation that a fragmentary vascular system is not in a primitive condition but is in a state of degeneration appears to be warranted by a survey of vascular systems in the animal series, and by the a priori argument that a vascular system must be efficient as a circulating and distributing apparatus in order to afford the advantage necessary for the operation of natural selection. The probable steps of the primary or ascending evolution of a vascular system do not include a condition in which large vessels are present without capillaries or are in free communication with the cœlom.

From the examination of the pharyngeal bars we may now proceed to that of the median ventral tract of the pharynx, which it is convenient to call in toto the "endostyle," the name being justified by the undeniable identity of the peculiar median ridge of epithelium with that which is recognised by this name in the Ascidians.

Below the endostylar epithelium, as shown in the series of sections, figs. 4—9, Pl. XXXVI*B*, there is a chitinous plate which has hitherto remained undescribed. It consists of right and left moieties, and is segmented; that is to say, it thins out and disappears for a brief space at intervals. This endostylar skeleton, in fact, consists of a number of pieces following one another, corresponding in number to the primary gill-slits, each piece being composed of a loosely-joined overlapping right and left half. The endostylar skeletal plates rest on the ends of the chitinous arches formed by the union of the adjacent anterior and posterior halves of the furcal extremities of the rods of the primary gill-bars.

Whilst the furcal ends of the rods of the primary bars of the pharynx penetrate thus deeply below the endostyle, the rods of the tongue-bars are shown, by the drawings referred to, only to reach the margin of the endostylar tract. A large cœlomic space exists beneath the endostylar chitinous plates, and around the furcal ends of the primary rods. This space is seen by following the sections to communicate freely with two structures of the pharyngeal bars, viz. (*a*) with the soft-walled pharyngo-pleural fold of the primary bars, and (*b*) with the cavity of the hollow chitinous rod of the tongue-bars.

The contractile endostylar artery or cardiac aorta is seen in the sections either in the middle line or a little to the right or to the left. A large branch is given off from it to each primary bar, but the sections have not enabled me to trace the vessel actually into the bar or along its length. No vessel is given off to the tongue-bars.

I have not observed in sections of the endostylar region the muscular tissue which Schneider has described as existing there, and I doubt the correctness of his observation.

The structure of the deep part of the rods of the primary bars, where their bifurcate extremities lie below the chitinous plates of the endostyle, is remarkable. The substance of the rods consists of a reticular tissue with scattered nuclei, and the chitinous matter appears to be superficially deposited around this axis (see figs. 4—9, Plate XXXVI *B*). It is necessary to bear in mind that in speaking of the rods of the pharyngeal skeleton as "chitinous," one is using that term without strict justification, in order to indicate not the specific chemical substance "chitin," but a certain density and horn-like character in a structureless skeletal deposit. The "chitinoid" substance of the pharyngeal bars and of the endostylar plates of Amphioxus appears to be a special form of the subepidermic lamina of the connective tissue, which is seen everywhere affording firm support to the columnar cells of the body-surface. It is to be regarded as a product of the connective tissue, and it is there, fore intelligible that the furcal ends of the chitinoid rods should gradually pass over into a gelatinous reticular form of connective tissue.

The Supra-pharyngeal Cœlom and its Perienteric Extension.—I have but little to say in regard to this space. It is sufficiently obvious in sections, and contains a coagulable fluid. It is continued down the plaits or folds of the primary pharyngeal bars, and communicates through them with the cœlomic space surrounding the branchial aorta, viz. the endostylar cœlom. Anteriorly it ends blindly, acquiring a considerable lateral and at last a ventral extension along the inner walls of the epipleura, in the prægenital region of the body. Posteriorly, in the region where the perforations of the pharynx cease, it forms a narrow space surrounding the intestine, and in the post-atrioporal region expands to a much increased proportionate volume. It ceases at the anus, and similarly it is not traceable anteriorly beyond the sphincter oris. Its relations are seen in the drawing (Pl. XXXIV, fig. 1).

The perivascular space of the dorsal aortæ has been alluded to above in connection with those vessels. I will merely say again that they appear to me to be real spaces, and not artifacts, and that I have not traced any opening into them. They unite when the aortæ unite and form a single space.

The perigonadial cœlom is, according to the observations and speculations of Kowalewsky, Rolph, and Hatschek, a detached downward continuation of the pharyngo-dorsal cœlom, carried downwards with the down-growing epipleura, and subsequently shut off from the pharyngo-dorsal cœlom above. In such a section as that given in Pl. XXXVI we can see that a slight horizontal splitting of the connective tissue would place the two spaces in communication.

The Metapleural Lymph-Spaces.—These and the lymph-boxes or spaces of the fin-rays appear to be traceable to the original myocœlomic pouches.

The metapleural lymph-canals are large, well-developed spaces, containing coagulable lymph. Their existence has been denied by some observers in consequence of the action upon them of absolute alcohol, which shrinks up the metapleura and obliterates the space. Johann Müller thought that they opened anteriorly, each by a pore, but it is admitted now that no such pores exist.

The most important fact about the metapleura which has been hitherto overlooked is that their space is abolished, and their very existence as upstanding longitudinal ridges ceases when the gonads attain their full size at the breeding season. The stretching of the epipleural wall leads to a complete flattening of the metapleura, as shown in Pl. XXXV, fig. 4. It seems not improbable that the albuminous fluid contained in the metapleural canals may serve as a final supply of nutriment for the enlarging gonads.

Were there any "ventral canals" such as have been supposed to exist by nearly all writers on Amphioxus, this would be the place, viz. in association with the metapleural canals, in which to discuss them. Stieda's specimens and figures showed the whole of the epithelium of the plaited ventral wall of the atrium "blistered" or raised from the subjacent connective tissue. Accordingly he described the existence of a pair of large ventral canals lying right and left between the two metapleura. Rolph, Langerhans, and Schneider, described not a single pair of canals but a number running parallel to and corresponding with the longitudinal ridges of the surface. The spaces which are frequently seen in this position are really between the connective tissue and the epidermis and are due to differential shrinking. Rolph indicates canals below the layer of connective tissue in this position, that is, between the ventral transverse muscle and the connective tissue. It appears to me that no such canals exist. The insertion of the fibres of the transverse muscle into the connective tissue, and the excessive contraction of the muscle under the influence of reagents, causes a deep plaiting of the connective tissue and a tearing and separation of natural adhesions in most specimens. But in such a preparation as that drawn in (Pl. XXXVI *A*, fig. 2,) we see that there is no splitting of the connective tissue in the median ventral area corresponding to the splitting which forms the lymph-space of the metapleura. The artifact canals which have been mistaken for natural ventral canals (Bauchcanäle) lie in one of two situations either of which is impossible for a natural lymph-space, viz. between the connective tissue and the epidermis or between the connective tissue and the muscular fibres.

The Lymph Spaces of the Dorsal and Ventral Fin-Rays.—I have already spoken of these above in treating of the fin-rays. Hatschek ('Anatom. Anzeiger,' August 15th, 1888), has shown that they are originally in continuity with the myocœlomic pouches (see Plate XXXVI*A*, figs. 6 and 7). Rolph, Langerhans, and Schneider have recognised and described the character of the "fin-ray boxes" or lymph-space compartments and their epithelial lining. Fine canals passing from these spaces have been described and are noted by Schneider. Such fine spaces and irregular canals are to be seen in the thick connective tissue which forms the substance of the fin-membrane (as distinguished from the fin-rays) of the caudal fin and præoral lobe. Schneider states that he has not seen a coagulum in the "fin-ray boxes," but such a coagulum occurs not unfrequently.

The Intra-notochordal Lymph Canals.—In sections of Amphioxus may be observed dorsally and ventrally within the notochordal sheath a clear space, the natural shape and extent of which appears to be that given in Pl. XXXVI. The dense laminar structure of the notochord is here deficient and replaced by short intercrossing fibres. Adequate staining with hæmatoxylin reveals a number of small nuclei in the neighbourhood of these spaces in connection with the fibres. Other nuclei are seen in a series on either side in the lower half of the notochord, but nuclei do not occur deeply nor generally within the notochord (see Pl. XXXVI*A*, fig. 1). The dorsal and ventral space thus seen in sections are due to the existence of a dorsal and ventral lymph-holding space which have not sharply defined walls, but are bounded by loose fibres. The more dorsal of these canals was first observed by Kossmann (**14**), and the somewhat smaller ventral one by Camille Moreau

(15). It is not my immediate purpose to discuss the histology of the notochord of Amphioxus, but to determine the existence of natural spaces within that animal which have to be distinguished from artifact spaces. The two intrachordal canals are connected with the most violent distortions of the shape of the notochord under the influence of reagents. The greater or less rapidity with which osmotic currents are established and the alternative distension or shrinking of the canals leads to such alterations in the shape of the notochord as those shown in outline in Pl. XXXVI *B*, fig. 10, *a*, *b*, *c*, *d*.

The sudden and powerful contraction of the muscles attached to the connective-tissue sheath of the notochord, and to the connective-tissue septa passing from it, also helps in the distortion of the notochord. The extent of the distortion caused by the contraction of the muscular fibres of the myotomes, may be judged of by the large spaces which are frequently left where they have torn themselves away from the connective tissue. The undoubtedly artifact spaces thus produced must be distinguished from the remarkable spaces between myotomes and notochordal sheath, and again between myotomes and neural skeleton, which have been described by Schneider, and are related to the roots of the anterior and posterior spinal nerves.

In view of the undeniable distortions of the notochord which the muscular strains and the distension or shrinking of the intrachordal canals must produce, I feel great hesitation in admitting as natural structures the remarkable apparent perforations of the sheath of the notochord, found dorsally on either side of the dorsal intrachordal canal at regular intervals; and according to Moreau, who first described them under the name "godets," placing the dorsal intrachordal canal in communication with the neural canal, within which the nerve-cord is contained.

I am inclined to consider the "godets" of Moreau as naturally existing tubercles of the notochordal tissue, as shown in Pl. XXXVI *A*, fig. 1*f*. But it appears to me that they do not completely perforate the sheath of the notochord, nor penetrate into the neural canal. They appear to be segmentally arranged in pairs at regular intervals, as described by Rolph, Langerhans, and Schneider; and for the present their morphological and physiological significance is altogether unknown.

The Neuraxial Canal.—The central canal of the myelon of Amphioxus must necessarily be cited in an enumeration of the spaces within the body of that animal. Expanding to the form of an oval cavity in the anterior region of the myelon, which may justly be called the brain, the canal is extremely small and narrow throughout the rest of the cord. It does not become the seat of any distorting action in preserved specimens, and therefore no more need be said of it here.

It is worthy of remark that a perineural lymph-space,[1] which in some Vertebrates is largely developed between the myelon and the neural skeletal sheath or spinal canal, seems to have no existence in Amphioxus. The connective-tissue tube or canal which forms the skeletal protection of the myelon in this animal seems to adhere closely to the nervous tissue, and it is rare to find, even under the influence of the most violent action affecting other parts of its structure, a separation of the skeletal sheath and the contained nervous tissue. In rare cases I have observed such a dislocation, as also a case in which the true notochordal tissue was also displaced or shrunk from its investing connective-tissue sheath (in fig. 1, Pl. XXXVI *A*).

The Intra-skeletal Lymph-spaces of the Myotomes and Myocœlomic Pouches of the Head.—Professor Hatschek, in the 'Anatom. Anzeiger,' August 15th, 1888, has published an extremely valuable though brief account of his observations on the development of the myotomes and skeletal tissue of Amphioxus. Two of Professor Hatschek's figures are reproduced in Pl. XXXVI *A*, figs. 6 and 7. The division of the primary segmental cœlomic pouches each into a dorsal portion (protovertebra or Urwirbel) enclosing the "myocœl," and a ventral portion (lateral plate or Seitenplatte) enclosing the "splanchnocœl," is described.

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[1] In front of the termination of the nerve-cord there is a small space within the neural sheath filled with coagulable liquid (Pl. XXXVI *A*, fig. 3*b*).

It is pointed out that the dorsal pouches enclosing each a "myocœl" undergo the following modification :—The parietal wall (subjacent to the epidermis) becomes cutis, and is called, therefore, the "cutis-layer," whilst epithelial cells of the mediad wall (adjacent to the notochord) become individually elongated and converted into muscle-cells. The cavity of the myocœl remains for a time, and the muscular tissue is a truly epithelial tissue.

Professor Hatschek does not deal with the adult animal. It may therefore be stated that the myocœl cavities totally disappear in the full-grown Amphioxus, excepting at the extremities of the body. Some of the spaces, which are invariably to be found in transverse sections of Amphioxus between the connective tissue and the muscular masses of the myotoms, are artifact, and due to the contraction of the muscular fibre. These spaces can be distinguished from the natural intraskeletal lymph-spaces of the myotomes (first described and figured by Schneider) by the fact that they are not limited by connective-tissue epithelium.

Professor Hatschek states that after the myocœl is formed a secondary pouch forms by a folding inwards and upwards of the ventral wall of the myocœl, which, as development advances, makes its way as a double fold between the notochord and the muscle-layer, whilst at the same time the pouch grows downwards between the lateral plate (the cavity of which is the splanchnocœl) and the epidermis. The cells of this offset of the myocœl pouch give rise to the skeletal tissue, which invests the notochord and the nerve-cord, as well as the fin-rays, the cavities of which are part of the myocœl, whilst it also furnishes the fascia to the muscle-fibres. The arrangement is explained by the two diagrams in Pl. XXXVI *A*, figs. 6 and 7, copied from Hatschek's paper. In the adult Amphioxus the space between muscle fascia and notochord sheath persists as a series of large lymph-holding spaces in connection with the roots of the spinal nerves (see Pl. XXXVI and Pl. XXXVI *A*, fig. 1). The walls of the space become adherent in parts, but leave considerable regions as cavities filled with blood-lymph (Blut-haltende Raum of Schneider). Their exact shape and extent in each myotome requires further careful study by means of a series of sections, since they are liable to distortion by osmotic action.

In the first three or four myotomes, which are traversed in transverse sections in the neighbourhood of the eyespot and olfactory pit, it appears to me that the myocœl cavities are permanently preserved, and that the spaces as seen in Pl. XXXVI *A*, figs. 3, 4, 5, are not artifact but natural. The myocœl has, in fact, never been obliterated by the adhesion of its opposite walls.

The Atrio-cœlomic Funnels or Brown Canals.—These structures, which I discovered and described in 1874, are a pair of short wide funnels placed in the 27th myotome, right and left, at that region where the pharynx narrows to form intestine. The wider end of the funnel is open to the atrium, the narrower end is within the dorso-pharyngeal cœlom, and the axis of the funnel is parallel with the long axis of the body (see Pl. XXXV, fig. 1). It is difficult to decide whether the narrow end is actually perforate, but I am inclined to think that it is. The funnels are lined internally by the pigmented epithelium which characterises the atrial wall. Each funnel adheres by one side to the roof of the dorso-pharyngeal cœlom, as shown in the transverse section, Pl. XXXV, fig. 2. The wall of the funnel is formed by a firm connective tissue with nuclei in addition to the lining layer of pigmented epithelium. The funnels always exhibit longitudinal folds as though they were capable of dilatation.

It depends on the size of the Amphioxus whether these funnels are met with in sections with many bars to the pharynx, or in sections where the bars and slits are few in number and extent, and the pharynx reduced in volume. Probably in quite young Amphioxus the atrio-cœlomic funnels do not occur in the same vertical plane as any of the gill-slits, but as growth goes on the pharynx extends farther back, carrying with it the wide mouths of the funnels, the pointed extremities of which remain in the 27th myotome. Thus in a full-grown specimen a vertical plane passing through the narrower part of the atrio-cœlomic funnels will also cut the deepest and most fully developed region of the perforations of the pharynx as shown in Pl. XXXVI.

I am not able to offer any suggestion as to the function of the atrio-cœlomic funnels, based on positive characters. Their inner cell-lining appears not to be glandular, and their connective-tissue tunic is equally devoid of any special characters. It is possible that they may serve either to admit water to the cœlom or to remove the cœlomic liquid under conditions of tension. The structure and position of one of these funnels render it probable that were there greater tension of liquid in the cœlom than in the atrium its walls would be pressed together and the funnel closed. On the other hand, were there greater tension of the sea-water contained in the atrium than of the cœlomic fluid, the funnel would be dilated and sea-water would flow into the cœlom until the tension was equalised.

Morphologically, the atrio-cœlomic funnels are paired short tubes placing the cœlom in continuity with the exterior, for the atrial cavity is morphologically external surface. In so far they correspond with the abdominal pores of craniate Vertebrata. Mr. Bateson (2) has shown that they have a remarkable correspondence in other respects to the collar-pores of Balanoglossus. The collar of Balanoglossus is, like the epipleura of Amphioxus, an outgrowth of the body wall. It may be compared to a dice-box open at each end and fused with the body wall of the Balanoglossus (over the head of which it has been pushed) all round the inner surface of its constricted middle third. It is thus in fact not one collar but two, one having its free circular margin directed forward and the other having its free circular margin directed backwards. The anterior collar surrounds and conceals the mouth and the base of the proboscis; the posterior collar surrounds the commencement of the pharyngeal perforated region and overhangs two or three gill-slits. It is on the under surface of this posterior collar that the pair of collar-pores are placed.

The epipleura of Amphioxus, like the double collar of

Balanoglossus, are fused to the body wall immediately behind the mouth. In front of this region they project as an almost complete collar, the so-called præoral hood; behind it they are not short and annular in direction, as in the posterior collar of Balanoglossus, but are extended horizontally so as to enclose the whole perforate region, and their free margins fuse together below the ventral wall of the pharynx. Still we can easily imagine a reduction of the epipleural folds of Amphioxus which would give us them in the form of an incompletely annular fold, overhanging only the three or four anterior gill-slits. Now, if we consider the position of the atrio-cœlomic funnels, we find that they are in the base of the epipleural folds, and therefore, with the reduction and shrinking of the epipleura, would come to lie very much in the position occupied by the collar-pores of Balanoglossus.

Whether the atrio-cœlomic funnels of Amphioxus, the collar-pores of Balanoglossus, and the abdominal pores of Craniata are to be considered as modified nephridia, is a question upon which I am not prepared to enter. Our conception of the nephridium as a unit of structure common to all Cœlomata, is at the present moment undergoing development and extension. But whilst we now refer to this category the genital ducts of Arthropoda and Mollusca, as well as glandular tubes with excretory functions, and whilst our notions as to the limitation of the number of nephridia in one individual or one segment are greatly modified, we must be careful not to assume too hastily that every opening in the body wall of a cœlomate animal communicating with its cœlom, is necessarily the opening of a nephridium. It is not impossible that so wide a generalisation as this may be established, but in the meanwhile it seems possible to distinguish such apertures as the dorsal pores of Lumbricus from nephridial openings, and so long as the former are not shown to be related by origin to nephridia, it will be necessary to admit the existence of a category of pores which have not, and never had, any relation to " a specialised tubular portion of cœlom, the lining cells of which have an excretory function." The words in inverted commas constitute the definition of a primitive or typical nephridium if we add to them these additional words, "the tube opening at one end on the surface of the body, at the other into the general cœlom." We recognise a variety of modifications of this primitive structure, more especially the loss of one or both of the openings of the tube, and the cessation of excretory glandular activity on the part of its lining cells. We can even admit the dwindling of the tube and its total disappearance, with survival of the external aperture only. But in all these modifications we start with the conception of a tubular modification of part of the cœlom, open to the exterior, and renal in the function of its lining cells. A pore which has had no such antecedent history is not nephridial, nor to be classed with nephridial structures.

It appears to me that we have not at present any grounds for assigning the atrio-cœlomic funnels of Amphioxus to either category. It is not improbable that the developmental history of the later stages of the Amphioxus-larva will furnish the necesary data.

The Connective Tissue.—I am desirous of saying a few words about the connective tissue of Amphioxus before concluding these observations.

In Plate XXXVI I have, for diagrammatic purposes, coloured the connective tissue and the gonad-cells of a uniform purple tint. Nevertheless we can readily distinguish in Amphioxus varieties of the connective tissue differing from one another in density and massiveness. The varieties pass over into one another at several points. One of the most important statements that can be made about all of them is that, like the other tissues of Amphioxus, they differ very greatly from the correspondingly placed tissues in other Vertebrates, and do not closely resemble those of any other animal. I am not acquainted with any chemical examination of either the connective tissues or the notochord of Amphioxus.

The structural varieties presented by the connective tissue of Amphioxus may be enumerated as (1) the lamellar; (2) the gelatinous; and (3) the cartilaginoid. When we examine well-stained specimens of Amphioxus we find that the nuclei of the cells which give rise to these varieties of skeletal substance are always arranged in simple layers, in fact are epithelial in character, and, as Hatschek (**16**) has recently shown, are in fact the epithelia bounding the primitive myocœl pouches or their outgrowths, as explained above (see Pl. XXXVI *A*, figs. 6, 7, copied from Hatschek).

Beneath the epidermis we find a dense lamina supporting the epithelial cells; beneath this, again, a softer, less dense gelatinous substance, and more deeply a second very delicate lamina, on which we find the connective-tissue cells. These four laminæ constitute the cutis. The cells of the deepest layer are the only cells of the connective tissue (see Pl. XXXVI *A*, fig. 1), and must be regarded as the matrix-cells of the various layers of skeletal substance superficial to them.

In the expanded regions of the median fin at the two extremities of the body the substance of the fin is formed by the gelatinous tissue, which is excavated by small irregular canals and spaces clothed with the epithelial connective-tissue cells. Thus a cartilaginoid tissue is produced, no longer a plane lamelliform deposit, but a tissue which increases in three dimensions (see Pouchet, this Journal, vol. xx, p. 421).

The thickened mass of cutis bounding the outer wall of the metapleural canal is formed by an increase in the gelatinous layer, which not only is thickened but contains numerous fibrillæ.

The fin-rays consist of a fibro-gelatinous substance, which is invested by an epithelial layer. The fin-ray boxes or compartments are, according to the important observations of Hatschek, survivals of the myocœlomic pouches, and are, at one time (as they are permanently at the extremities of the series) simple cavities lined with the myocœlomic epithelium. In the floor of the cavity beneath the epithelium the fibro-gelatinous fin-ray is formed, and gradually grows up into the compartment clothed with the epithelium. There are no canalicular spaces in the fin-ray, and no cells sunk in its substance.

The skeletal tissue which surrounds the notochord and forms the intermuscular septa and neural sheath, is, like all the rest, of epithelial origin, according to Hatschek. A special diverticulum of the myocœlomic pouch pushes its way, at an early stage of development, between the muscle and the notochord, and also descends between the epidermis and the lateral plate (see Pl. XXXVI *A*, figs. 6, 7). This outgrowth is called by Hatschek the sklerotome.

It is indicated in the adult by a layer of connective-tissue cells of epithelial character, which surround the notochord, and a second layer, which rests on the surface of the muscular mass facing the notochord. Between the two was originally a space continuous with the myocœlomic pouch. This space is obliterated in part, but in part persists as the intra-skeletal or myoskeletal lymph-spaces of the myotomes. The disposition of these layers of cells will be best understood by a comparison of Hatschek's figures and the drawing of a well-stained section of an adult Amphioxus (Pl. XXXVI *A*, fig. 1).

The sheath of the notochord deposited between the epithelial cells and the proper notochordal tissue is similar to the cutis in structure. Next to the notochordal tissue forming the innermost layer of the sheath is a dense, highly-refringent substance, which gradually passes over into a more distinctly laminate layer (corresponding to the gelatinous layer of the cutis), and then follow the cells. In some preparations the staining of these two layers is very different; in others they are not distinguishable from one another.

The dense innermost layer has been described by some observers as the cuticle of the notochord, just as the dense lamina below the epidermis is regarded as being formed by the epidermis cells. I am, on the contrary, inclined to reckon both to the connective tissue, and do not find in the adult Amphioxus any recognisable and distinct notochordal cuticle, though such may exist in the embryo.

The lamination of the connective tissue, both of cutis and notochord, will be best understood by the examination of figures 1 and 2 in Pl. XXXVI *A*, as interpreted by the important diagrams of Hatschek, which are reproduced side by side with them.

A curiously modified tract of connective substance is to be observed forming that part of the notochordal sheath which is attached to the dorsal wall of the pharynx (Pl. XXXVI *A*, fig. 1 *x*.). It has an irregular granular appearance, quite distinct from that of the connective substance in any other region, excepting a similar tract on the upper median surface of the notochordal sheath (*y*. in same figure).

The reticular tissue with nuclei which forms the axis of the furcal portions of the primary bars in the endostylar region of the pharynx seems to be distinct in character from all the other skeletal tissues of Amphioxus (Pl. XXXVI *B*, figs. 4 to 9).

The Notochordal Tissue.—The series of vertical laminæ which build up the notochord of Amphioxus have often been described and figured. I desire here merely to draw attention to the disposition of nuclei within the notochord as shown in well stained preparations. There are no nuclei in the position described by Moreau (15) towards the axis of the notochord; the nuclei are confined to two perfectly definite regions. In a transverse section a series is seen lying in a single row near the circumference of the notochord, and extending along the inferior third of its area. A second smaller group of nuclei is seen dorsally on either side of the dorsal intrachordal canal. I have already referred to the superior and inferior intrachordal canals. I may again state here that the notochordal tissue does not appear to me to form itself any cuticle or investing sheath. Such a cuticle may exist in the embryonic condition before the connective-tissue sheath is developed, but it would be difficult to attribute any part in the formation of the adult notochordal sheath to a delicate envelope of the kind, owing to the enormous increase in the bulk of the notochord.

Summary.—The present memoir by no means professes to be a monographic treatment of Amphioxus nor even to deal exhaustively with parts of the structure of that animal. It must be regarded as a contribution to the knowledge of Amphioxus, detailing a few new facts, offering evidence towards the decision of some doubtful questions, and above all pointing out a number of matters in which further observation is needed in order to clear up uncertainty. The chief points brought to notice are—

1. The number of the myotomes, of the dorsal fin-rays, of the ventral fin-rays, of the præoral cirrhi.

2. The size and importance of the post-oral tentacles, or tentacles of the sphincter oris.

3. The non-existence of the so-called "ventral canals" beneath the plaited ventral wall of the atrium.

4. The actual existence of the metapleura and metapleural lymph-canals, but their obliteration during complete distension of the atrium.

5. The actual existence as natural spaces of (*a*) the fin-ray compartments, (*b*) dorsal and ventral intrachordal canals, (*c*) the intraskeletal lymph-spaces of the myotomes.

6. The structure of the gill-bars and endostyle.

7. The position and form of the atrio-cœlomic funnels or brown-canals, now figured for the first time.

8. The general form of the body as corrected from distortion by reagents, and the disposition of parts as shown in a reconstructed dissection.

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EXPLANATION OF PLATES XXXIV, XXXV, XXXVI, XXXVI*A*, & XXXVI*B*,

Illustrating Professor Lankester's "Contributions to the Knowledge of Amphioxus."

PLATE XXXIV.

FIG. 1.—Semi-diagrammatic drawing of a dissection of Amphioxus lanceolatus. The animal is resting on the dorsal surface: the ventral half of the body has been separated by a horizontal cut, reaching on each side from near the mouth to the anus, and has been thrown over to the left side of the animal. The perforated region of the primitive body wall exposed by thus removing the epipleura has been severed from its median dorsal attachment and pulled over to the animal's right side, the dislocation being aided by cutting through the body transversely. The pharyngo-dorsal cœlom right and left of the median attachment of the pharynx to the notochordal sheath is thus exposed, the deeply folded wall formed by the pharyngo-pleural pouches being cut through. The lining membrane of cœlomic spaces is everywhere coloured blue; other surfaces are left either colourless or of brownish tint. The

drawing is intended to show especially the relation of the pharyngo-pleural pouches to the pharyngo-dorsal cœlom, the position and relations of the atrio-cœlomic funnels ("brown-pigmented canals"), and the post-atrioporal extension of the atrium as a cæcal tube running side by side with the intestine as far as the anus. A rod, *E*, is introduced through the atriopore into the atrial chamber, and a second rod, *F*, is passed from the post-atrioporal enlarged cœlom through the natural passage into the peri-enteric cœlom of the præ-atrioporal region. The letters are *a*, *d*, *d'* indicate the parts similarly marked in the transverse sections figs. 3 and 4; *v.* marks the folded cut edge of the body wall corresponding to the pharyngo-pleural pouches of the primary bars of the pharynx.

FIG. 2.—Diagrams of sections through the lines *A B* of Fig. 1.

FIG. 3.—Diagrams of sections through the lines *C D* of Fig. 1.

FIG. 4.—Amphioxus lanceolatus viewed from the right side, and magnified about five times linear. The animal is represented as nearly as possible in its living proportions and shape; the oral hood and tentacles are expanded, the atrial cavity is dilated, and the atriopore open. The drawing shows the number of the myotomes, sixty-two (this is probably an exceptional number, sixty-one or even sixty being more frequent); the number of the oral tentacles, the number of the dorsal and ventral fin-rays, the number of the gonads, the position of the atriopore and the anus.

FIG. 5.—Amphioxus lanceolatus viewed from the ventral surface. The specimen is the same as that drawn in Fig. 4, and the drawing is intended to show especially the plaits of the ventral epipleural surface, the position of the metapleura, the double series of ventral fin-rays, and the form of the præoral hood.

PLATE XXXV.

FIG. 1.—Untouched sketch of a horizontal section through the region of the atrio-cœlomic canals. The section is in a plane passing below the notochord and just cutting the top of the pharynx and the cæcum. It shows the two atrio-cœlomic funnels, with their widely open posterior mouths and their narrow anterior terminations, the left a little in front of the right.

FIG. 2.—Untouched sketch of a vertical section passing through the two atrio-cœlomic funnels. The division of the muscular fibres of the myotome into two groups, a deeper and a more superficial, is seen on the left side. The two sets of fibres are separated by connective tissue, but the distinction does not depend, as the lettering would imply, on the direction of the fibres themselves but on the arrangement of the groups of fibres; in both groups the direction of the actual fibres is essentially longitudinal.

FIG. 3.—Untouched sketch of the section in which the atrio-cœlomic funnels were first observed. The Amphioxus had been hardened by Kleinenberg's

picro-sulphuric solution, followed by alcohol, and was not treated with any staining reagent; consequently the brown pigment of the atrial tunic, which was richly developed in this specimen, was very obvious, as shown in the figure. Artifact spaces, together with the natural lymph-spaces in the neighbourhood of the notochord and nerve-cord, have produced a distortion of this region. The space marked "artifact space," on the left of the figure, is incorrectly labelled, being probably a natural lymph-space (myoskeletal lymph-space) slightly distended by the action of reagents.

Fig. 4.—Untouched sketch of a section through the branchial region of a female Amphioxus at the breeding season. The specimen was treated with Müller's fluid, followed by alcohol, and is remarkable for the great distension of the epipleura by the enlarged gonads, leading to obliteration of the metapleural ridges and canals and of the ventral plaits. The pharynx was badly preserved, and the sub-notochordal region much distorted. The artist has represented these parts in a rough and undetailed way.

Fig. 5.—Diagram of a portion of the body of Amphioxus, from which the notochord, roof of the pharyngo-dorsal cœlom, and upper part of the myotomes have been removed by horizontal section, so as to show the atrio-cœlomic funnels in position. A rod is passed from the peri-enteric cœlom into the pharyngo-dorsal cœlom.

Fig. 6.—Enlarged transverse section of an atrio-cœlomic canal, to show the cell structure, after staining with hæmatoxylin.

Fig. 6′. A piece of the same before staining.

PLATE XXXVI.

Diagram of a transverse vertical section through an adult female Amphioxus at the region of the atrio-cœlomic funnels. The muscular tissue is coloured yellow, the connective tissue and gonad cells purple, the hypoblastic cell-layer and notochord green, and the atrial epithelium light brown; the epidermis and nerve-cord are uncoloured, as also are the clots present in the metapleural canals, the fin-ray space, the pharyngo-dorsal cœlom, the myoskeletal lymph-spaces, and the dorsal aortæ.

The drawing is intended especially to show the form and position of parts when corrected from drawings of actual sections, so as to allow for local shrinking and distortion. The correct estimation of the spaces found in sections between the skeletal sheath of the notochord and the muscular tissue, and again between the latter and the neural skeletal tube and its skeletal crest, is exceedingly difficult, and has perhaps not been altogether rightly carried out. It has been necessary to select a particular section for illustration, the myo-skeletal lymph-spaces and the position of the inter-muscular septa being necessarily different in each one of a series of sections traversing a given segment of the organism. The section selected shows part of a posterior nerve-root and a portion of a group of anterior nerve-roots. The small lymph-space to the left of the neural crest appears to be part of one of a series (alternately right and left) not in continuity with those situate below the nerve-roots. The lymph-space below the posterior nerve-root on the right, and that below the anterior nerve-root on the left, are parts of corresponding spaces lying asymmetrically on each side of the skeletal tissue of the notochord-sheath and nerve-tube. The relation of the anterior nerve-fibres to the deep layer of the myotome is seen on the left side, but probably the correct and undistorted relation of these parts is not quite exactly ascertained (see Rohde, 17). The division of the more ventral portion of the myotomes into two groups of fibres, separated by delicate connective fascia, is prominently shown.

The continuity of the gelatinous layer of the cutis between the ventral epithelium and the transverse muscle, and the consequent absence of "ventral canals," is prominently shown.

The median artery of the endostyle is not drawn. This is an omission which is rectified by the series of sections in Pl. XXXVI *B*, Figs. 4 to 9.

PLATE XXXVI *A*.

Fig. 1.—Portion of a section through the notochord and adjacent region of Amphioxus. The specimen had been stained with logwood solution. Some of the structures shown are named in full on the drawing.

The letters have the following signification:—*a*. Artifact space, produced by the shrinking and tearing of muscular fibres from their attachment to the muscle fascia. *b*. Left myoskeletal lymph-space, between the fascia of the muscle of the myotome and the skeletal sheath of the notochord. Whether this space is opened out by the action of reagents, or is in its natural condition, is uncertain. In either case it represents the similarly situated space of Fig. 7, which represents an early larval condition. *c*. Similar space of the right side. *d*. Upper or para-neural portion of the myoskeletal lymph-space, which is shown by other sections to be in continuity with *b*. It contains a clot. *e*. Similar space of the right side, elsewhere in continuity with *c*. *f*. One of the "godets" of Moreau, or dorsal tubercles of the notochordal tissue. *g*. Artifact space caused by the shrinking of the notochordal tissue from its connective-tissue sheath. *h*. Dorsal canal of the notochord, with nuclei and trabeculæ. *i*. Ventral canal of the notochord. *k*. Thin connective-tissue septum (fascia), separating the inner from the outer group of muscle-fibres of the myotome. *l*. Ventrally placed nuclei of the proper notochordal tissue. *x*. Peculiar granular tract of the connective-tissue sheath of the notochord, lying above the plane of adhesion of the pharynx. *y*. Similar but smaller tract of granular-looking tissue at the opposite face of the notochord.

Fig. 2.—Portion of a transverse section of Amphioxus, to show the metapleur and the region of the supposed "ventral canals" (non-existent). The various structures shown are named on the drawing. A small artifact space is seen between the transverse muscle and the thick gelatinous layer of the cutis, which is similar in position and origin to larger rents which have led to the erroneous inference of the existence of "ventral canals." The nuclei of the transverse muscle and the vertically fibrillated non-nucleated structure of the gelatinous layer of the wall of the metapleur are noteworthy. The same fibrillated structure is seen in the gelatinous layer of the cutis in other sections through other parts of the body wall, especially where the transverse intermuscular septa join the sub-epidermic cutis.

Figs. 3, 4, 5.—Three vertical sections through the anterior extremity of Amphioxus, the first in front of the termination of the nerve-cord, the second through the olfactory pit, and the third through the eye-spot. The drawings were made by Mr. Herbert Thompson, M.A., in the zoological laboratory of University College.

a. Fin-ray lymph-space. *b.* Cavity of the neural sheath or skeletal tube in front of the termination of the nerve-cord, occupied by a clot. *c.* Anterior nerves in transverse section. *d.* Notochord. *e.* Sub-notochordal lymph-space, probably similar in nature to the dorsal fin-ray lymph-space. *f.* Irregular lymph-spaces lined with connective-tissue epithelium, excavated in the gelatinous tissue of the dorsal and ventral fin-plates. *g.* The ventral præoral fin-plate, becoming here the right half of the præoral hood. *h.* The unequally developed left-side outgrowth, which becomes the left half of the præoral hood. *i.* The ciliated olfactory pit, an inversion of the epidermis of the left side, connected with a short olfactory bulb or nerve given off from the left side of the nerve-cord. *k.* The wall of the nerve-cord enclosing the enlarged neur-axial canal. *l.* The eye-spot, consisting of distinct spherical granules of brown-black pigment. *m.* The unobliterated myocœlomic pouch of the first myotome, identical with the cavity marked *m.* in Fig. 7. *n.* The muscular epithelial cells of the mediad wall of the pouch. *o.* The myocœlomic pouch of the second myotome.

Fig. 6.—Diagram of a transverse section through an early larval condition of Amphioxus, showing the division of the primitive cœlomic pouches into a dorsal myocœl and a ventral splanchnocœl. The origin of the cutis from the peripheral and of the muscular tissue from the mediad wall of the myocœl is indicated. From Hatschek.

Fig. 7.—Diagram of a transverse section through a later larval condition of Amphioxus, showing the origin of the skeletal tissue from a secondary pouch, "the sklerotome," which grows out from the myocœl and pushes its way between the notochord and mediad muscular wall of the primitive myocœl, and downwards between the wall of the splanchnocœl and the epidermis. From Hatschek.

PLATE XXXVI*B*.

FIG. 1.—Transverse section of a "primary bar" of the pharynx of Amphioxus.

FIG. 2.—Transverse section of a "tongue bar" of the pharynx of Amphioxus.

Letters in Figs. 1 and 2.—*al.* Left inner epithelial band. *ar.* Right inner epithelial band. *am.* Median inner epithelial band. *col.* Columnar lateral cells, with long cilia. *n.* Superficial nuclei. *n'.* Deeper nuclei (? all epithelial or some mesoblastic). *sept.* Clear septal tissue. *Bl. vess.* Supposed blood-vessel, connected in the primary bar with the lateral branches of the median endostylar artery, and ending blindly at the ventral extremity of the tongue bars; probably connected dorsally in both to the dorsal aortæ. *Rod.* The chitinoid skeletal rod, bifid in the primary bar, hollow in the tongue bar. *fiss.* Fissure, due to the bilateral origin of the rod of the primary bar. *x.* Sporadic cavity of the rod of the tongue bar. *Cœlom.* The cœlomic cavity occupying the pharyngo-pleural extension of the primary bar, but enclosed in the rod of the tongue bar. *Cœl. ep.* Cœlomic epithelium of the pharyngo-pleural pouch of the primary bar. *atr. epith.* Atrial epithelium (epidermic), clothing the external face of both bars. *pig.* Lateral groups of pigment in the atrial epithelium of both bars.

FIG. 3.—*a.* to *e.* Various forms of the chitinous substance of the tongue bar, as seen in transverse sections. *f. to h.* Various forms of the chitinous substance of the primary bars.

FIGS. 4 to 9.—Six consecutive vertical sections across the endostyle of the anterior third of the pharynx of Amphioxus. The sections are numbered from behind forwards. The first section (Fig. 4) passes on the side marked "Right," through the junction of the anterior half of the fork of the rod of the primary bar *A* with the posterior half of the fork of the rod of the primary bar *B*. Opposite to this, on the side marked "left," the section traverses the actual fork of the rod of the primary bar *C*, at the point where a lateral vessel is given off from the median endostylar artery, and runs up into the fork (see Schneider's figure of the bars and blood-vessels, loc. cit.). The grouping of the epithelial cells is shown in all the figures; they are lettered in Fig. 9 as follows:—*al.* and *ar.* Right and left lateral epithelium (similar to that marked *al.*, *am.*, *ar.*, in Figs. 1 and 2). *bl.* and *br.* Right and left groups of less-staining cells. *cl.* and *cr.* Right and left interposed groups of darker-stained cells. *dl.* and *dr.* Mediad right and left groups of less-staining cells. *m.* Median group of darker-stained cells, with a special very long tuft of cilia. In all nine groups of cells.

In all the sections the chitin-like endostylar plates, immediately underlying the nine-zoned endostylar epithelium, are seen; like the chitinoid substance of the pharyngeal rods they are coloured yellow, having a slightly yellow tinge and highly refringent character in the actual sections. The bilateral character of these plates is clearly seen, also their connection with the rods, and their "thinning out" at intervals (*e. g.* Fig. 5, where the left endostylar plate is very thin, and Fig. 4, where it is practically absent).

Following the sections according to their numbering, we see in the second the median endostylar artery, with its clot coloured black for diagrammatic purposes. The section traverses a free portion of the primary bar belonging to rod *A*, and within the endostylar area we see the posterior half of rod *B* on the one side, and the anterior half of rod *C* on the other side.

In the third section (Fig. 6) we come across the junction of a tongue bar with the endostylar tract on the right side; whilst the primary bar belonging to rod *C* on the left side is seen much in the same relation as is the primary bar belonging to rod *A* on the right side of Fig. 4.

In the fourth section (Fig. 7) the tongue bar on the right side, and the primary bar on the left side, are cut more largely; whilst a tongue bar extremity is seen on the left side also.

In the fifth section (Fig. 8) the junction of the forks of two rods, *C* and *D*, is traversed on the left side (actual left, but right of the drawing); and the median artery is giving off a lateral branch to the incipient fork of the primary-bar rod *B*.

In Fig. 9 the lateral vessel is more largely involved, the tongue bar of the right side is cut through its free region, and the tongue bar of the left side is seen in apposition to the endostylar tract.

The whole series of figures serves to demonstrate the continuity of the cœlomic space of the endostyle, with the pouch of the primary bars and with the cavity of the hollow rods of the tongue bars.

Fig. 10.—*a*, *b*, *c*, *d*. Outlines showing various forms of distortion of the notochord, in transverse section, brought about by the action of reagents.

Fig. 11.—Section through the fin-ray lymph-space of the first dorsal fin-ray, to show the bilateral base of the fin-ray and its consequent similarity to the double fin-rays of the ventral series between atriopore and anus.

a. Epidermis. *b*. Outer lamella of cutis. *c*. Gelatinous layer of cutis. *d*. Spaces in gelatinous layer of cutis. *e*. Inner lamella, with nucleated cells of cutis. *f*. Right and left basal pieces of the fin-ray. *g*. Fin-ray lymph compartment. *h*. Neural sheath.

Fig. 12.—The twelve post-oral tentacles of Amphioxus or tentacles of the sphincter, seen from the post-oral surface. Drawn by Mr. Arthur Willey, student of University College, London, from a preparation made by him.

These tentacles depend from the oral sphincter (velum of Huxley and Langerhans) into the pharynx, and are provided with numerous special sense-organs described by Langerhans (5).

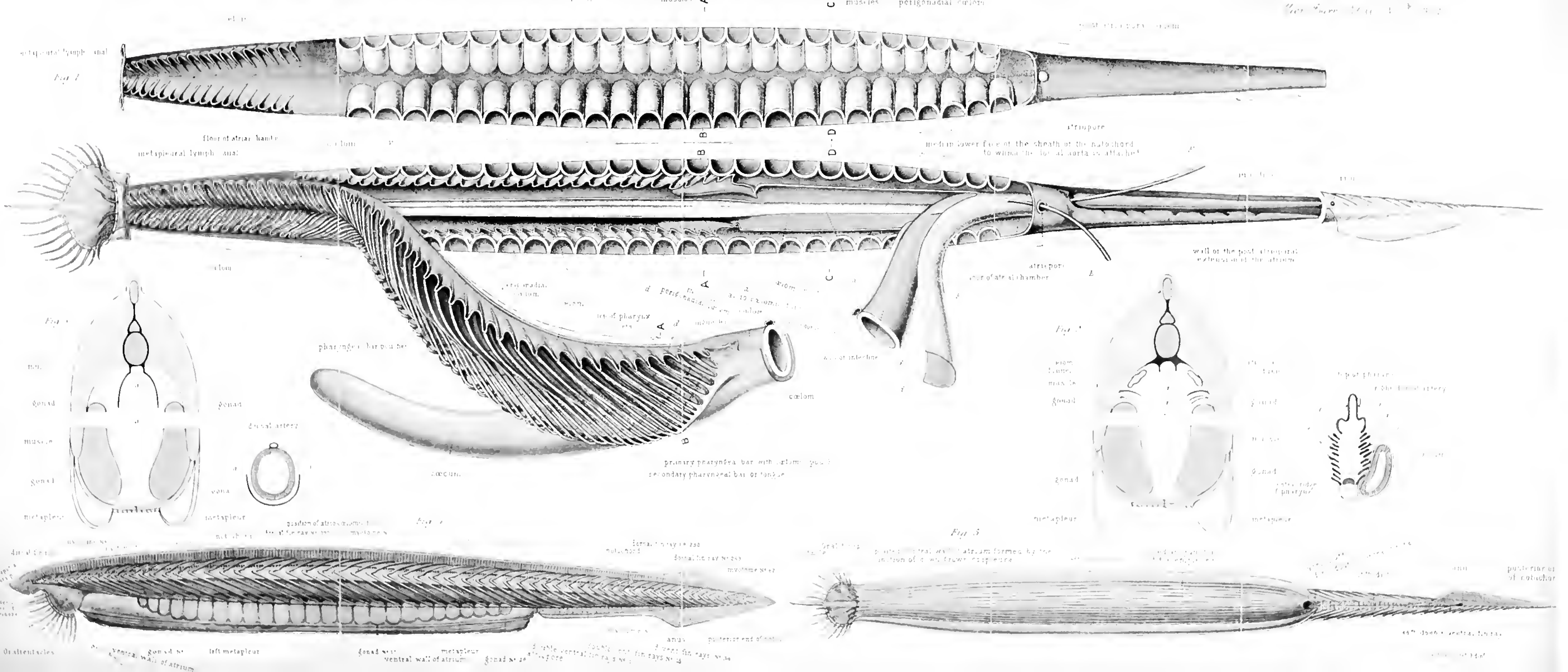


Fig 1
metapleural lymph canal
floor of atrial chamber
metapleural lymph canal
cœlom
B
B
A
C
D
D
C
muscles
perigonadial cœlom
atriopore
median lower face of the sheath of the notochord
to which the dorsal aorta is attached
wall of the post-atrioporal
extension of the atrium
atriopore
floor of atrial chamber
perigonadial cœlom
perigonadial cœlom
end of pharynx
pharyngeal bar
cœlom
cœcum
primary pharyngeal bar with
secondary pharyngeal bar or tongue
muscle
gonad
gonad
metapleur
gonad
muscle
gonad
dorsal artery
metapleur
metapleur
metapleur
gonad
muscle
gonad
gonad
Fig 4
notochord
myotome
dorsal fin ray No 250
myotome No 62
Oral tentacles
Ventral wall of atrium
gonad No
left metapleur
gonad No
ventral wall of atrium
metapleur
gonad No 26
double ventral fin rays
anus
posterior end of notochord
Fig 5
posterior end of notochord

Fig. 1.

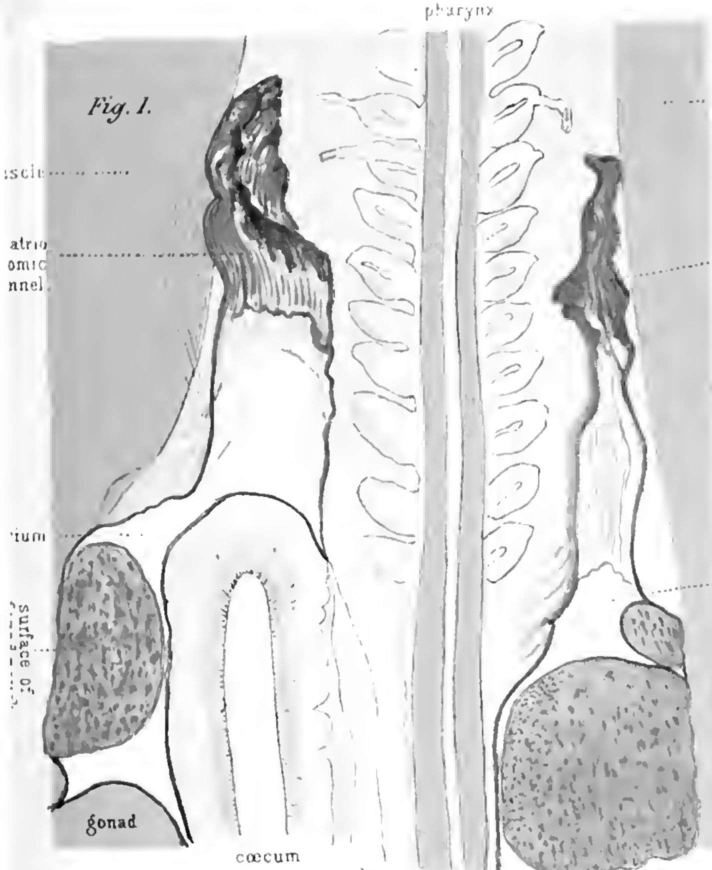


Fig. 2.

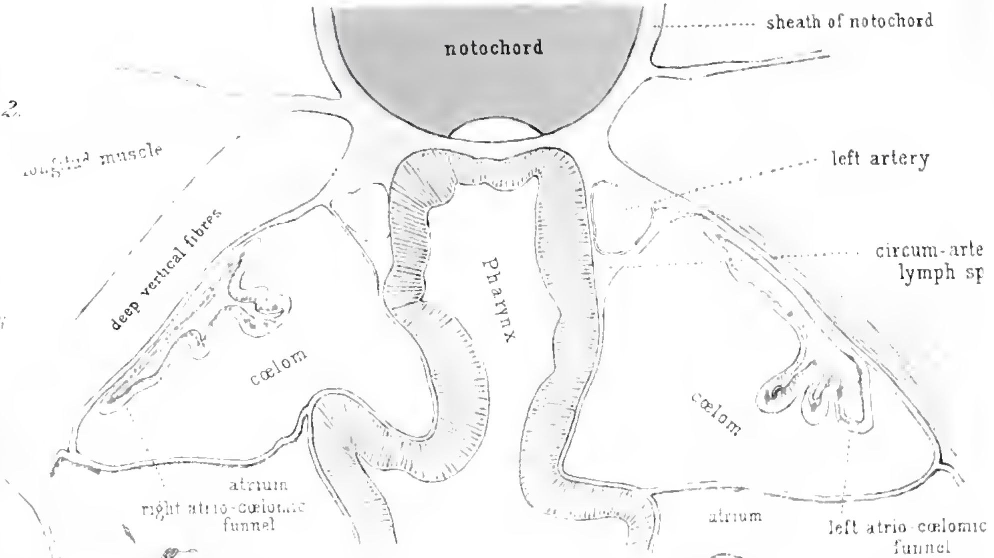


Fig. 4.

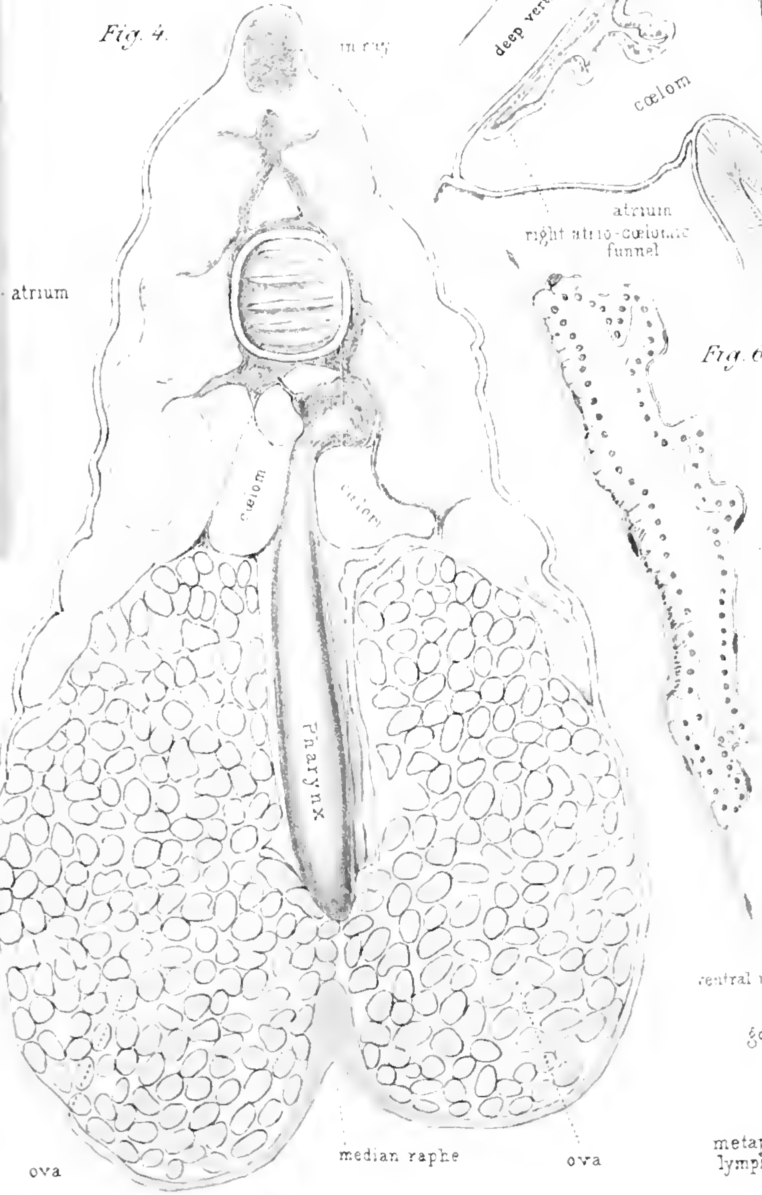


Fig. 6

Fig. 3. Fig. 6'

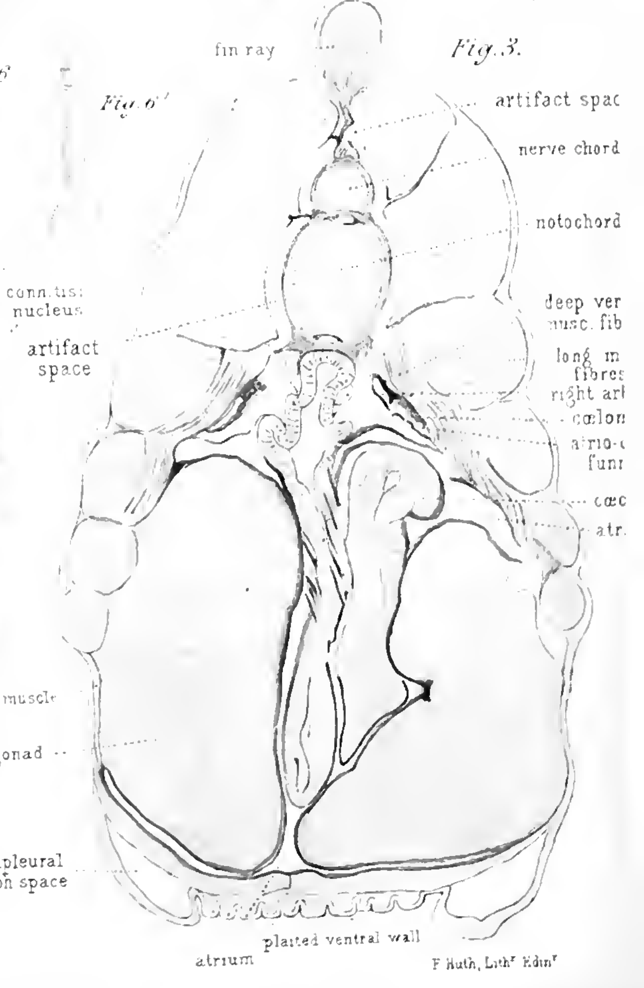
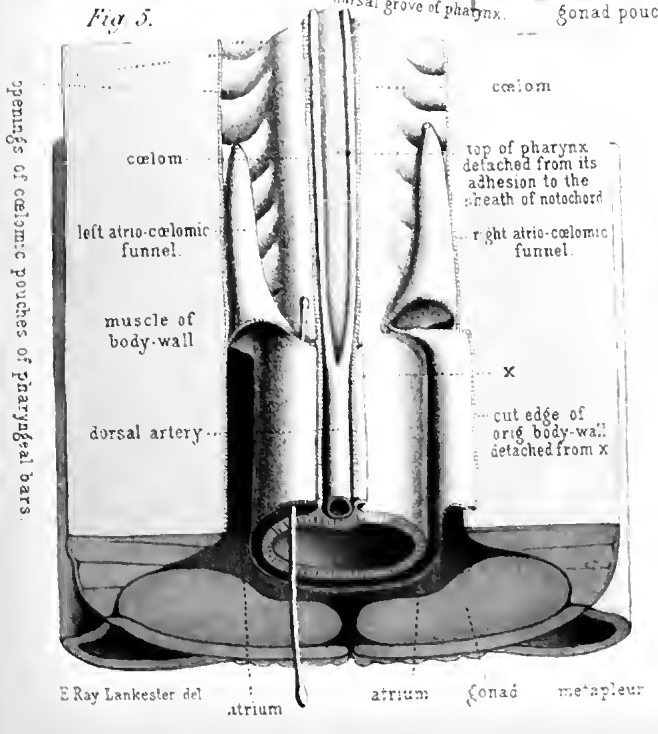


Fig. 5.



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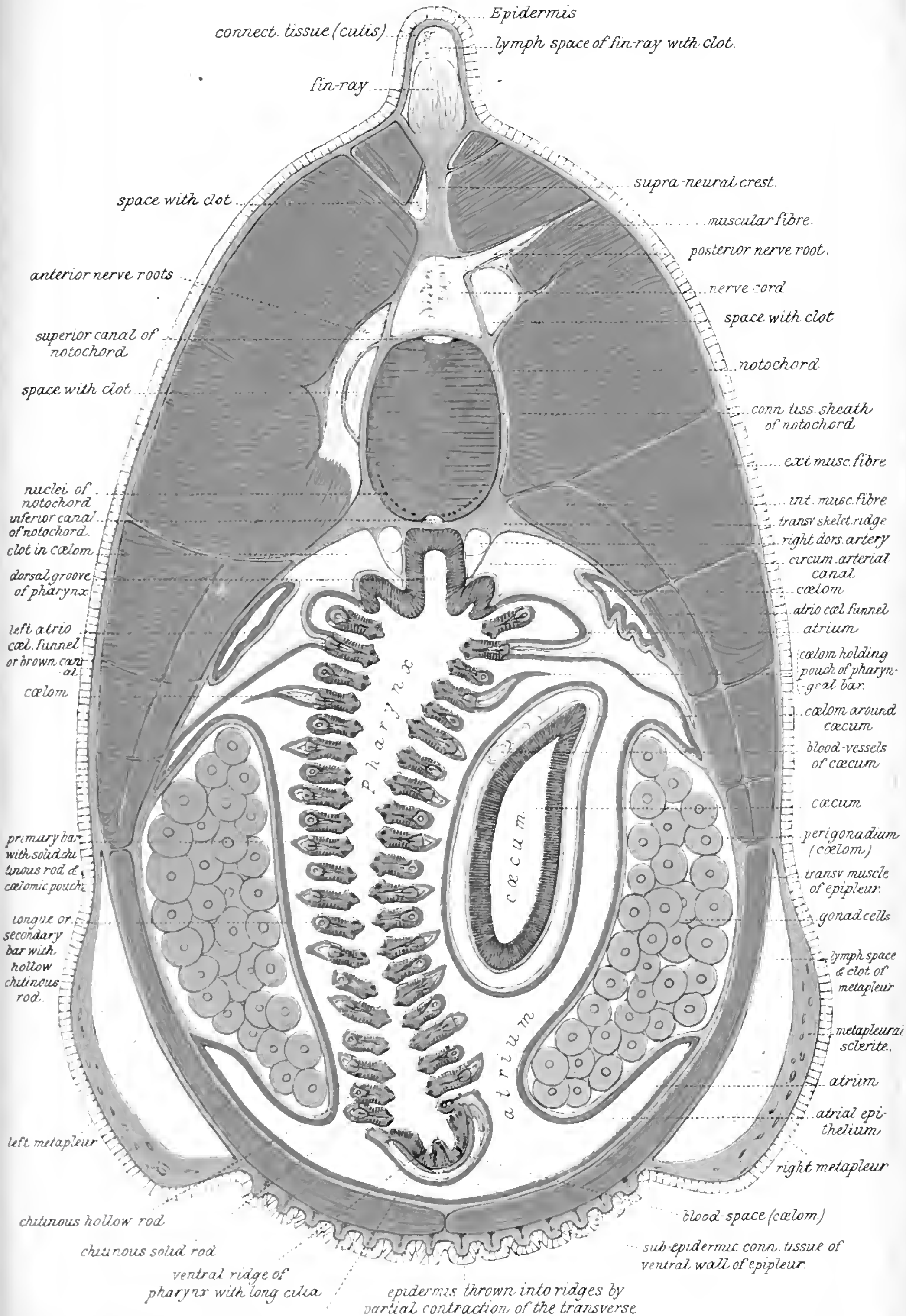

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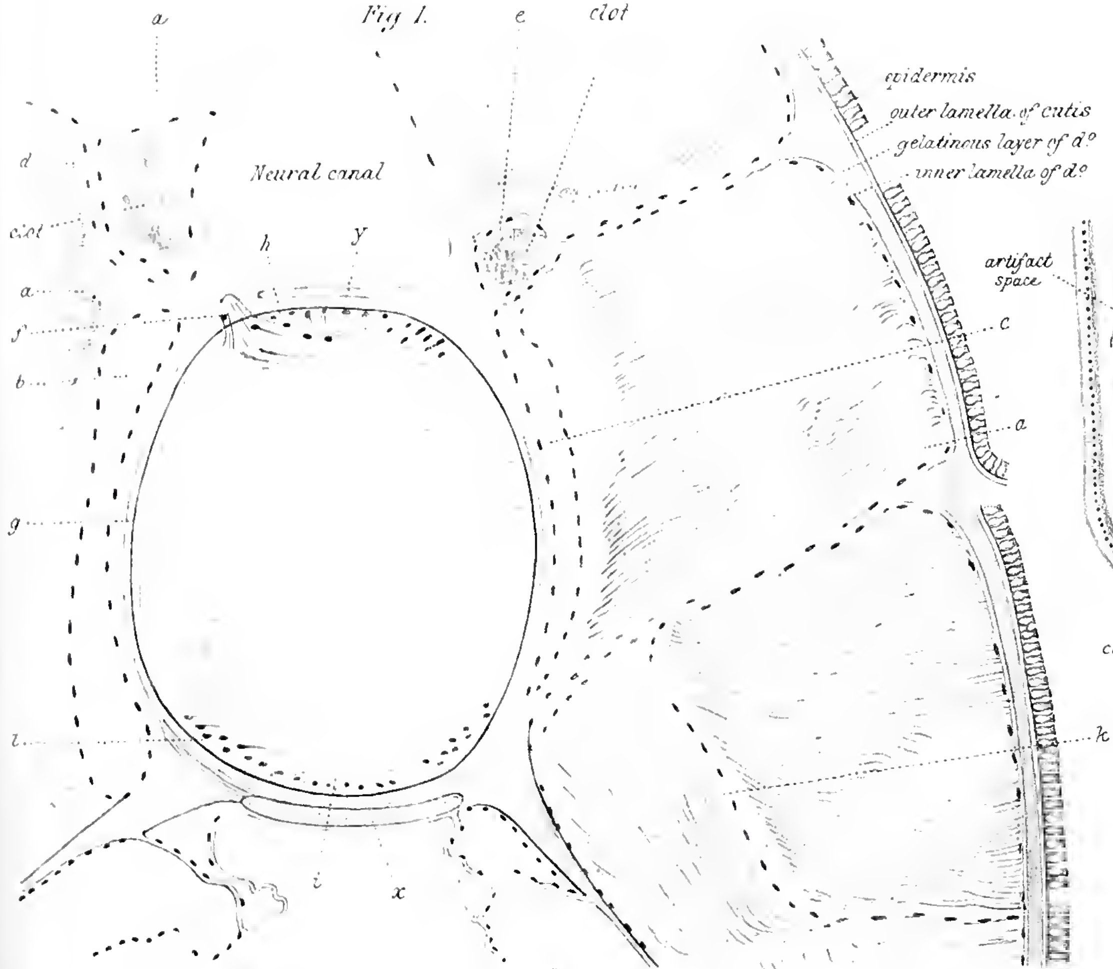

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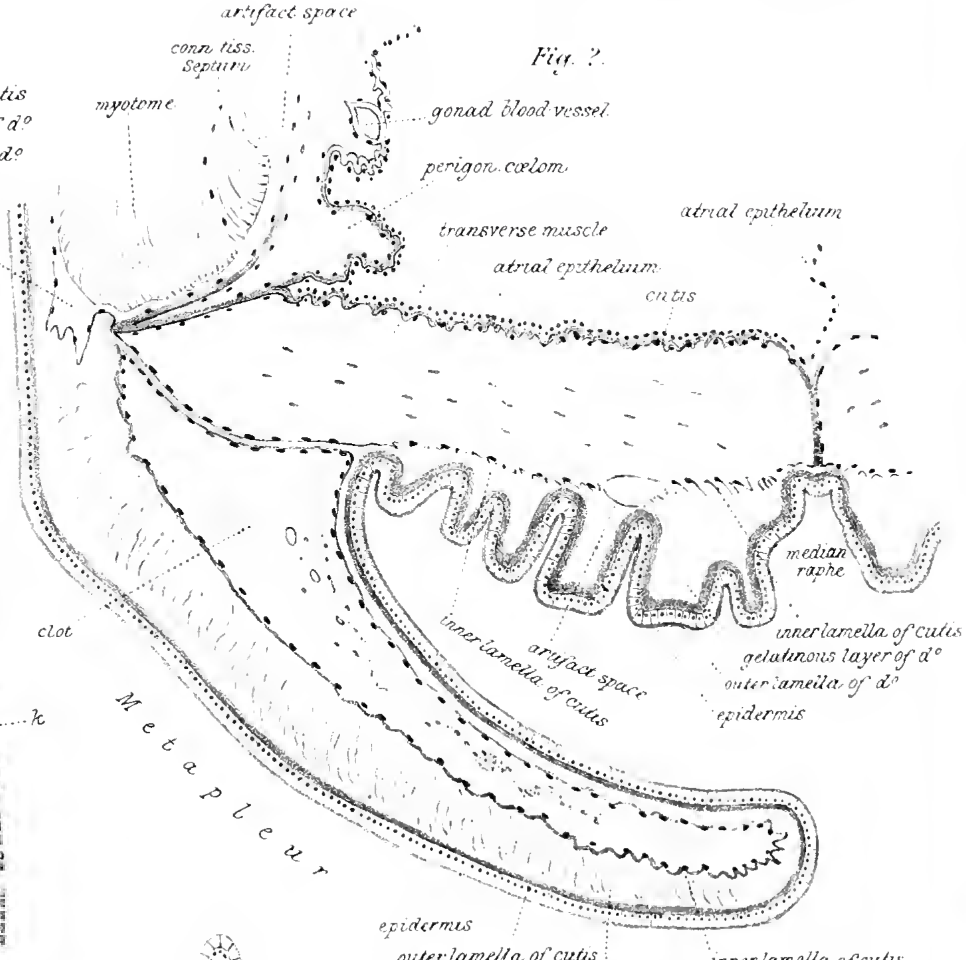

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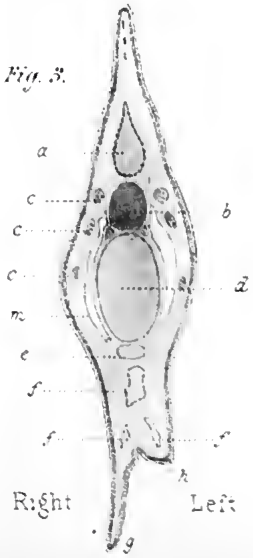

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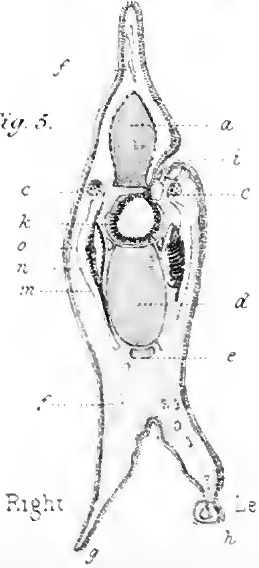


Fig. 4.

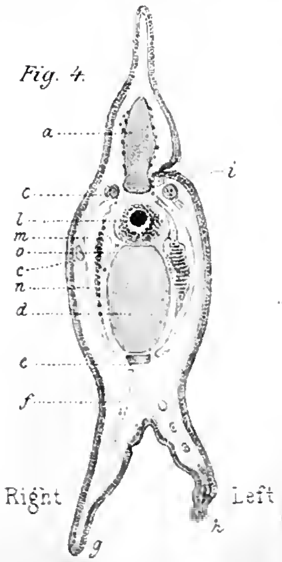


Fig. 7.

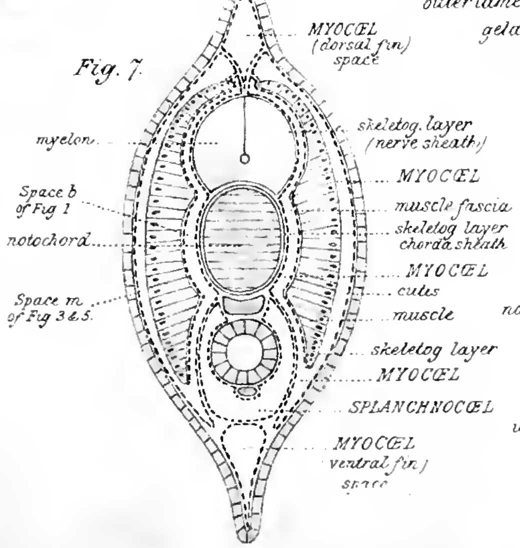
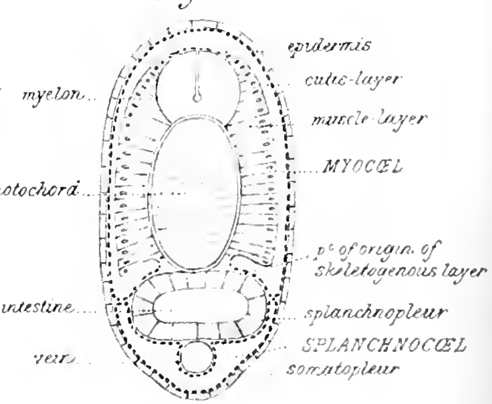


Fig. 6



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F. Huth, Lithʳ. Edinʳ.

Fig. 1

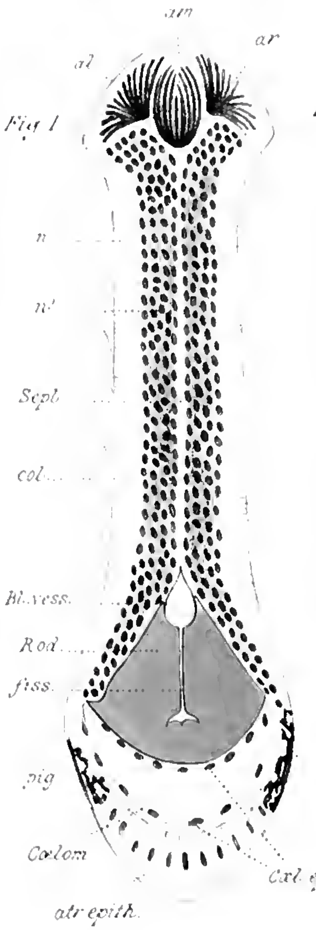


Fig. 2

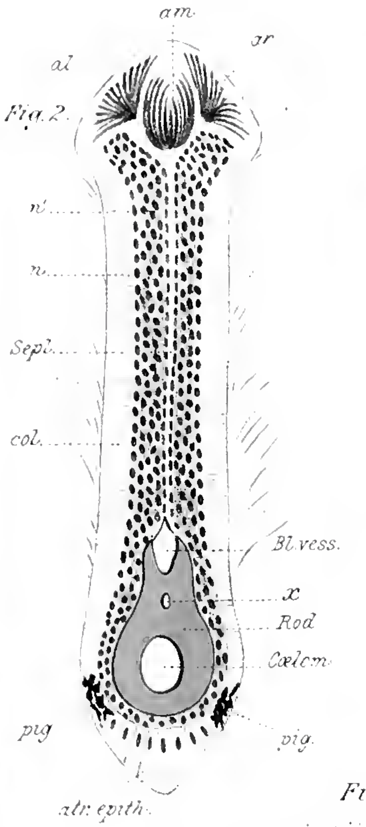


Fig. 3.

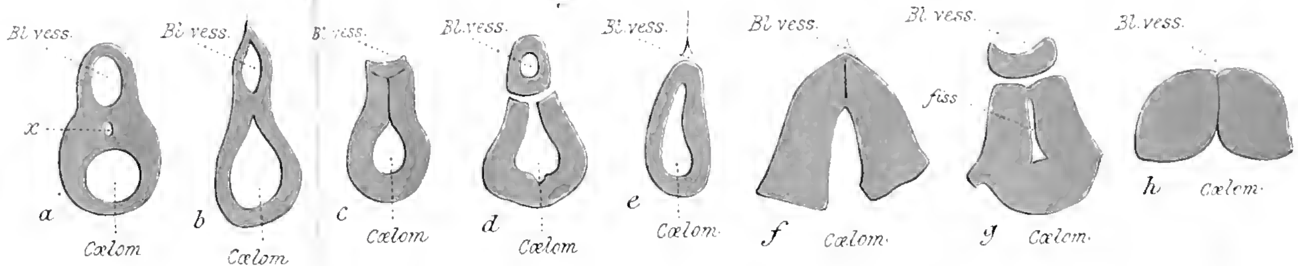


Fig. 10.

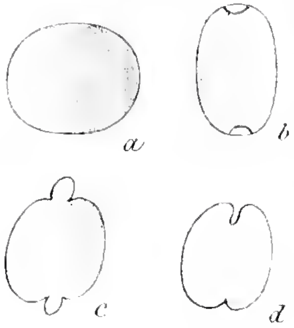


Fig. 4

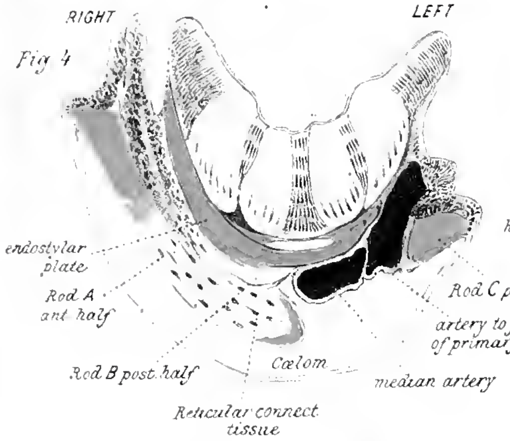


Fig. 7.

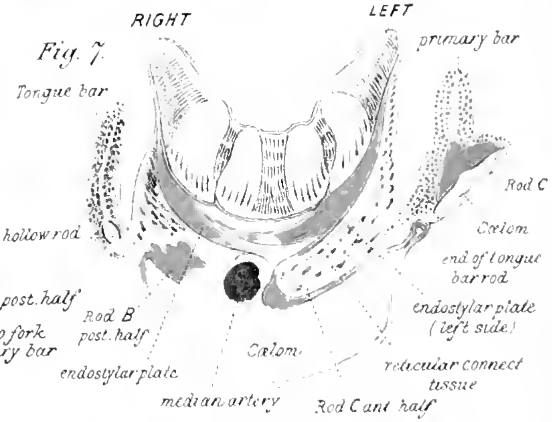


Fig. 5.

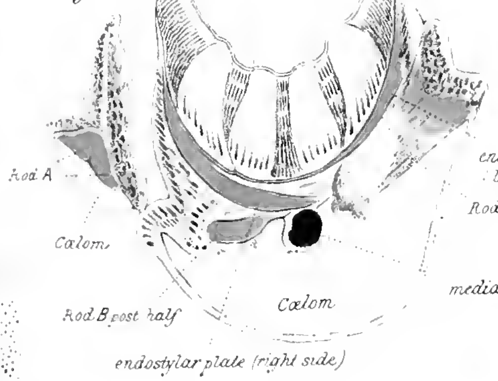


Fig. 8.

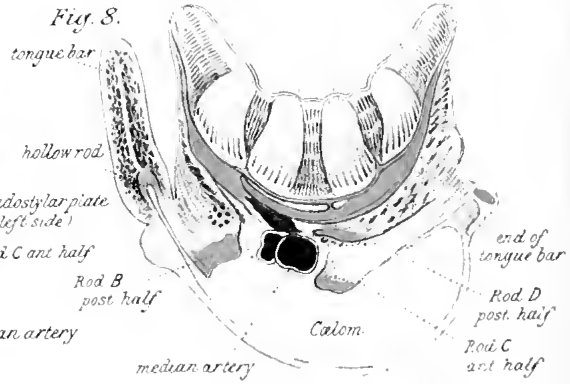


Fig. 6.

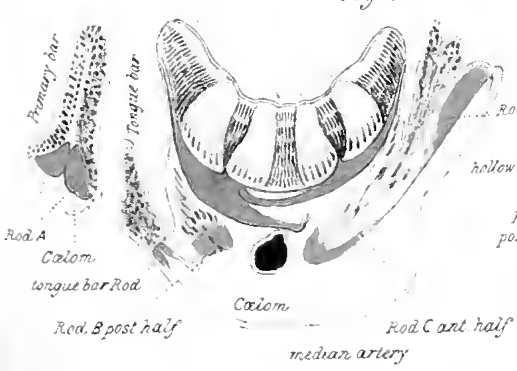


Fig. 9.

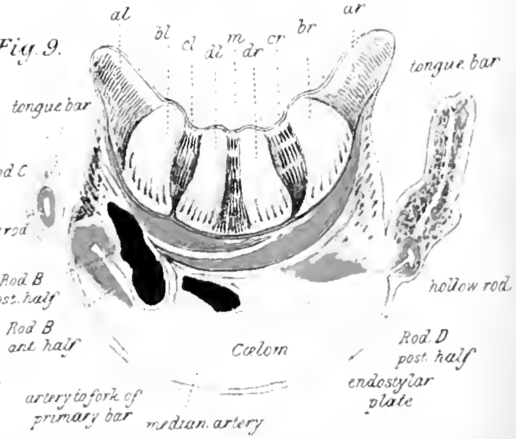


Fig. 11.

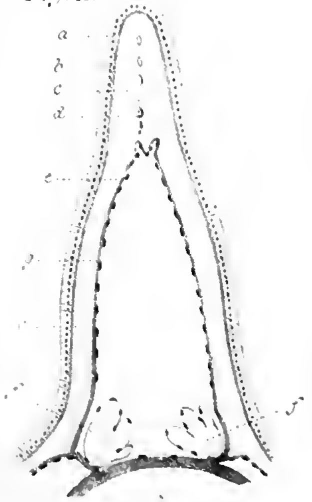
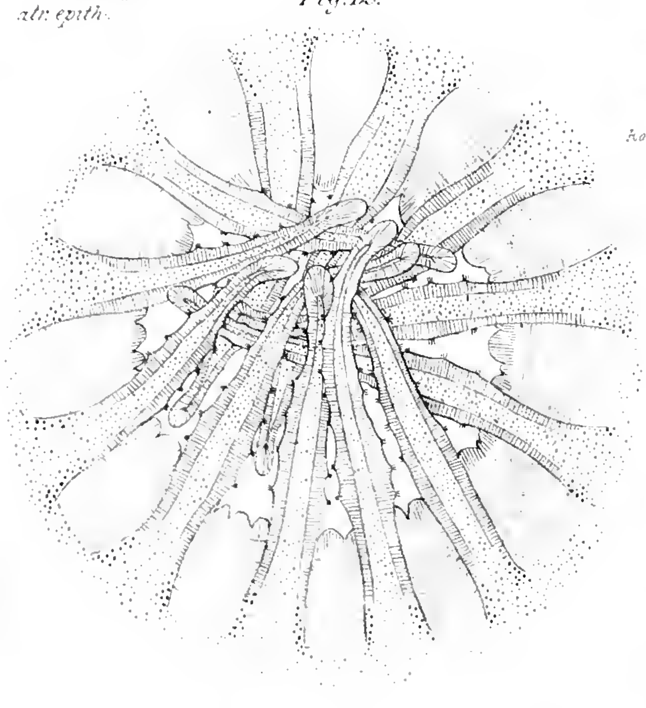


Fig. 12.



Ray Lankester del.

F. Huth, Lith^r Edin^r

Studies in the Embryology of the Echinoderms.

By

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Fellow of Trinity College, Cambridge.

With Plates XXXVII, XXXVIII, and XXXIX.

In the following pages I propose to give a comparative account of the structure and development of certain organs in young Echinoderm larvæ. I am not here concerned with the earliest stages (gastrula, &c.), nor with those later ones in which the pentamerous symmetry of the adult is already assumed, but only with that bilaterally symmetrical stage which is more or less clearly represented in all Echinoderm larvæ, and to which Semon (28) has given the convenient name "Dipleurula."

At this stage but few organs are developed, and one of them —the alimentary canal—is too similar in structure throughout the group to need any comparative description. I have therefore confined myself to the following points:

I. The primary divisions of the cœlom, starting from a stage in which at least two enterocœl pouches are already present.
II. The Hydrocœl: its development and connections.
III. The Skeleton, so far as it is developed in the dipleurula stage.

I. Primary Divisions of the Cœlom.

Up till quite lately only three main divisions of the cœlom were usually recognised in Echinoderm larvæ—the right and left enterocœls and the hydrocœl; for though some observers asserted the presence in Ophiurid and Echinid Plutei of a second hydrocœl, yet the existence of this was not generally accepted.

In my paper on Antedon (7) I showed that there exists in the larva of this animal a separate cavity (anterior body-cavity), median, or nearly so, with which the water-pore is related, and into which the hydrocœl subsequently opens by means of the water-tube (= stone-canal); and I pointed out the existence in Asterina gibbosa of an apparently homologous cavity. I shall now try to show that this cavity is always represented in Echinoderm larvæ, but it is not always unpaired, as in Antedon, a very distinct fellow to it on the right side being frequently visible. This condition, with two anterior enterocœls, I consider to be probably the most primitive, and I shall therefore begin my account with a description of those forms in which it obtains.

Ophiurids.—The youngest Ophiurid Pluteus I was able to obtain had already a pair of cavities lying beside the œsophagus, but none as yet beside the stomach; and was, in fact, in the stage described and figured by Metschnikoff (**18**, p. 21, pl. v, fig. 2). The only account we possess of the origin of these cavities is that of Apostolidés (**3**), who believes that both in Ophiothrix versicolor and in Amphiura squamata they are formed by delamination in the mesoblast. Since, however, he describes the gastral cavity of these forms as also formed by delamination, while Kowalevsky (**13**, p. 5) in Ophiura (sp. ?), Selenka (**27**) in Ophioglypha lacertosa, Balfour (**4**) in Ophiothrix fragilis, and Fewkes (**9**) in Ophiopholis aculeata, find it to be formed by invagination, we may be permitted to think cither that Apostolidés is mistaken, or that he has studied exceptional forms; and that in some Ophiurids, at least, the two cavities beside the œsophagus arise as pouches of the archenteron, as in other Echinoderms. In any case the homology of these cavities with the similarly placed pair in Echinids and Asterids is hardly likely to be disputed.

In the next stage observed there was present, in addition to the pair of cavities already mentioned, another pair beside the stomach. I was unable to trace the origin of this new pair, but I have no reason to doubt the correctness of Metschnikoff's statement (**18**, p. 21; **19**, p. 62) that they are directly derived from the first-formed pair.

At this stage (and possibly earlier) the left anterior enterocœl, which is not, as has been stated, a hydrocœl, opens to the exterior by a pore ("water-pore") at its posterior end on the dorsal surface of the larva. Examination of the living animal, under a high power, shows that this pore is formed by a single elongated cell, perforated throughout its length, and lined with cilia. It is important to notice that at this stage we have a larva with almost complete bilateral symmetry (broken only by the water-pore), and with two pairs of enterocœl pouches assuming a metameric arrangement.

In fig. 1 I have represented one of the earliest stages in the development of the hydrocœl, and one which has escaped the notice of previous observers. On the right side the anterior and posterior enterocœls remain as in the previous stage, but on the left side a third vesicle has now made its appearance between the two previously formed: this third vesicle is the hydrocœl. For a long time I remained in doubt whether it was derived from the anterior or posterior enterocœl; in the specimen figured, however, it was quite separated from the former though still connected with the latter; and in fig. 18 is shown, on a larger scale, part of a larva in which its walls are closely fused with those of the posterior enterocœl, while the anterior enterocœl (represented by a dotted outline) is apparently entirely distinct. These and other specimens have convinced me that the hydrocœl is derived from the left posterior enterocœl, though I confess this conclusion has surprised me, since, as we shall see, this condition is not found in any other group of Echinoderms. The stage just described is a very transitory one: almost immediately the hydrocœl separates itself completely from the posterior enterocœl, and, assuming an elongated form, pushes its way towards the anterior end of the larva, immediately ventral to the left anterior enterocœl. From the latter it is distinguishable by its more regular outline, the greater distinctness of its lumen, and the more refringent character of its walls; indeed, it is altogether so much more conspicuous an object than the overlying enterocœl, that it is easy to overlook the latter altogether, or to mistake it for a solid mass of mesoderm cells—an error into which previous observers appear to have fallen.

A section, through a larva in this stage, just behind the water-pore, is given in fig. 19, and confirms the observations made upon the living animal. It is true that in this section the lumen of the right anterior enterocœl is not seen; but this, when the small size of the cavity is considered, is not surprising. I have abundant evidence that the cavity still exists.

Echinids.—The first stage which concerns us here is that of the young Pluteus with two completely separated enterocœls lying beside the œsophagus; a satisfactory figure of this stage is given by Prouho (**24**, pl. xxiv, fig. 3). Whether these two cavities are separate from the first (**24**, p. 234), or whether they are at first united (**26**, p. 49), is a question which need not detain us now. Even at an early period the bilateral symmetry is rendered incomplete by the development of a ciliated pore (water-pore) at the posterior end of the left enterocœl.

The next stage in development is marked by the division of each of the primary enterocœl pouches into two lobes, one of which remains beside the œsophagus, while the other extends back to the side of the stomach. This was the latest stage observed by Prouho (**24**), but in all my larvæ (belonging to Echinus microtuberculatus, Strongylocentrotus lividus, Sphærechinus granularis, Echinocardium cordatum, and other unknown forms) each cavity soon divided completely into two, so that a stage was reached such as Metschnikoff (**18** and **19**) has already described, in which there exist two anterior and two posterior enterocœls, the only difference between my account and Metschnikoff's being that he describes the anterior enterocœls as "Wassergefässanlagen" (= hydrocœls), which I shall presently show to be incorrect.

But whatever name we may give to these cavities I am entirely in agreement with Metschnikoff as to the reality of their existence, which has been frequently questioned, or even denied. Thus Götte (**11**, p. 609) denies their presence in Spatangids, and asserts that the two primary enterocœl cavities simply shift their position down to the stomach, while part of the left one at the same time forms the hydrocœl. This view is also taken by Ludwig (**17**, p. 141), and apparently by Selenka (**26**), who does not otherwise account for the fact that the only two cavities noticed by him are at first situated beside the œsophagus, and afterwards beside the stomach.

Though Metschnikoff's account of this stage is therefore the most correct one yet given, yet in the next stage he has, as in his account of Ophiurids, fallen into error by confounding the hydrocœl with the anterior enterocœl; it must, however, be admitted that the phenomena are here even more difficult to make out, and that a stage is soon reached in which, but for the evidence afforded by the Ophiurids, the fundamental distinction between the anterior enterocœl and the hydrocœl could hardly have been recognised.

In fig. 8 is represented the earliest stage in which I have been able to determine the relations of the hydrocœl. It consists, as in Ophiurids, of a vesicle with thick and well-defined walls, lying between the anterior and posterior enterocœls on the left side; but it differs from its homologue in Ophiurids in that its cavity is already connected with that of the left anterior enterocœl. Whether it is derived from this anterior enterocœl or from the posterior one, as is stated by Götte (**11**, p. 609), Ludwig (**17**, p. 141), and Selenka (**26**, p. 49), is a question which, in spite of much time spent upon it, I am unable to answer satisfactorily. The latter is suggested by the analogy of the Ophiurids, but on the whole my observations seem to support the former, and to indicate that the communication above mentioned between the anterior enterocœl and hydrocœl means that they have never become entirely separated. However this may be, in considering the difference between Metschnikoff's account and nomenclature and mine, it is important to notice that on the right side of the œsophagus there still exists a cavity exactly comparable to that which I have called the left anterior enterocœl (except that it has no pore), whereas the structure to which I have here confined the term hydrocœl is entirely unrepresented on the right side.

Asterids.—In the young Bipinnaria we find beside the œsophagus a pair of peritoneal vesicles, one of which early opens to the exterior by a pore situated at its posterior end. Both vesicles soon extend back to the stomach, over which these posterior lobes spread dorsally and ventrally, while the anterior lobes, lying beside the œsophagus, have no such dorso-ventral extension; it is at the junction of the anterior and posterior lobes on the left side that the water-pore lies. It is clear that we have here the representatives of the anterior and posterior enterocœls of Ophiurids and Echinids, though they are not as a rule separated from one another.

In many forms of Bipinnaria and in Brachiolaria the two anterior lobes of the enterocœls grow forwards and unite in front of the mouth, and are then continued as a common cavity into the large præoral lobe; but they are always separate in young larvæ, and in certain forms of Bipinnaria described by J. Müller (**21**) and Metschnikoff (**18**, pp. 32—40) they never unite at all. I obtained a few examples of such a form at Naples, and they are so instructive that it will be well to describe their anatomy in some detail.

In fig. 14 one of these larvæ is represented as seen from the dorsal side. The hydrocœl is already present as a pouch opening into the left anterior enterocœl, though its exact mode of origin was not traced. But the great peculiarity of this larva lies in the fact that on the left side the anterior and posterior enterocœls are entirely separated from one another. In Asterina (**17**) there is a dorsal communication of these two cavities just above the hydrocœl and just behind the pore, and a ventral communication just below the hydrocœl;

the latter communication is absent in all the Bipinnariæ which I have examined, but the dorsal one is usually present. In the small form here figured, however, I convinced myself, both by observation of the living animal and by sections, that no communication existed between these two cavities at this stage.

It is interesting to notice that this larva gives us two characters, not possessed by other Asterid larvæ, in which it resembles the Plutei of Ophiurids and Echinids: (1) firstly, the anterior continuations of the enterocœls are never united in the præoral lobe; (2) secondly, on the left side there is a complete separation of the anterior and posterior enterocœls just behind the water-pore. No separation of the anterior and posterior enterocœls on the right side was ever observed. It should further be noted that in its external form this larva gives evidence of being primitive, in that it retains up to the time of metamorphosis the simple outline characteristic of all young Bipinnariæ, without developing the gigantic præoral lobe and elongated arm-like processes which so entirely alter the appearance of other Bipinnariæ in their later stages.

In fig. 13 is given a lateral view of the same larva, in which it will be seen that the hydrocœl occupies nearly the same position as in young Ophiurid and Echinid Plutei namely, between the anterior and posterior enterocœls; but in remaining open to the anterior enterocœl it approaches the Echinid rather than the Ophiurid condition.

The Bipinnariæ with a large præoral lobe and terminal fin (Bipinnaria asterigera), and Brachiolaria, do not differ much internally from the form just described, except in the already-mentioned communications (1) between the anterior and posterior enterocœls of the left side, dorsal to the hydrocœl, and (2) between the right and left anterior enterocœls; the latter is clearly secondary. But in Asterina, Ludwig (17) describes a very different arrangement; though, as I shall subsequently show, my observations do not entirely agree with his. According to him, the right and left enterocœls are from the first connected with a single large anterior cavity occupying the whole of the præoral lobe; and the hydrocœl, which arises as a pouch on the left side at the junction of the left enterocœl with the cavity of the præoral lobe, has at first a portion of the cœlom intervening between it and the wall of the stomach—a condition which I have not observed in any other Echinoderm. Subsequently the hydrocœl comes to lie close to the stomach, having, as already mentioned, a ventral as well as a dorsal communication between the anterior and posterior divisions of the cœlom (17, p. 147, pl. ii, fig. 37).

In a previous paper (7, p. 38) I put forward the view that the single large anterior enterocœl of Asterina might be primitive; but I ought to have remembered its formation in Bipinnaria and Brachiolaria by the fusion of two primarily distinct cavities. Now, the larva of Asterina is probably a modified Brachiolaria (17, p. 154), so that we shall be more correct in assuming that in this, as probably in many other points, Asterina exhibits a secondary and abbreviated form of development.

Crinoids.—The earliest formation of the enterocœl pouches and hydrocœl in Antedon rosacea (the only Crinoid yet studied), exhibits some peculiarities with which we are not at present concerned (see 5 and 7); we will pass at once to the stage in which the following divisions of the cœlom are present: (1) a single median anterior enterocœl (called "canal de sable" by Barrois). At the close of the free-swimming stage, this opens to the exterior at its posterior end by the water-pore, situated on the left side of the larva; (2) right and (3) left posterior enterocœls, one on each side of the stomach; these do not long retain their lateral position; and (4) the hydrocœl, on the left side, between the anterior and the left posterior enterocœls; at first it opens into the anterior enterocœl, but this communication is soon closed. Although this anterior enterocœl usually occupies a median position in the præoral lobe, I have little doubt that it is the homologue of the left anterior enterocœl of other Echinoderms, and, indeed, in many cases it lies distinctly on the left side.

Holothurians.—For the early stages of development of the cœlom in this group I must refer to the well-known accounts of Metschnikoff (18) and Selenka (25). In a well-developed Auricularia, we find a pair of enterocœls beside the stomach, and a single vesicle on the left side at the level of the œsophagus; this vesicle, which opens to the exterior by the water-pore, is usually looked upon as the hydrocœl, but I shall endeavour to show that it contains also the rudiment of an anterior enterocœl.

Fig. 22 gives a lateral view of this vesicle in an abnormal specimen which first attracted my attention to the subject: it will be seen that between the straight tube leading from the pore and the thick-walled inner portion (which subsequently becomes lobed, and is undoubtedly the hydrocœl), there intervenes a thin-walled section, which extends but slightly behind the pore, but is considerably elongated towards the anterior end of the larva.

In fig. 21 we have a dorsal view of the same part of another larva, showing that the thin-walled cavity has no great lateral extension. It is evident that this cavity has precisely the position and relations of the anterior enterocœl of an Echinid Pluteus, or of the small Bipinnaria above described; it is, therefore, important for us to see how far it is represented in normal larvæ. My attention was not called to this point till rather late in the season, when Auriculariæ were becoming scarce; but from time to time I managed to obtain a fair number of larvæ, and there was not one in which I was not able to recognise some vestige of this anterior enterocœl, though before noticing the abnormal one (fig. 22) I had never detected a trace of such a structure. The cavity is extremely variable in size, but fig. 23 represents what appears to be a fairly typical development, and is useful in illustrating the extreme difficulty of observation. Owing to the form of the larva, the only positions in which it is possible to get a steady and prolonged observation, give us a directly dorsal or directly ventral view; but in a dorsal view (fig. 23) the thin-walled anterior enterocœl lies directly over the thick- and refringent-walled hydrocœl, and is consequently extremely difficult to see, its component cells being hardly distinguishable from the surrounding mesoderm cells, which lie scattered over the surface of the hydrocœl, while other mesoderm cells (purposely omitted in this figure) collected round the water-pore and the tube leading from it ("pore canal") further obscure it. A lateral view (fig. 24) is far more satisfactory, but is by no means easy to obtain; the only method known to me is to place the larva in a watch-glass and roll it over until it assumes the required position; but of course it cannot then be kept perfectly steady, and drawing with the camera is impossible.

To the later stages of development, in which this cavity is still easily traceable, I shall return presently. Enough has, I think, been said to show that in Auricularia a cavity is present between the hydrocœl and the water-pore, which, though usually rudimentary, we have reason to regard as the representative of the left anterior enterocœl. We shall subsequently see that it is also present in Cucumaria, though perhaps not at such an early stage.

Summary and Conclusions.

Ophiurids.—Here we find two pairs of enterocœls, metamerically arranged. The anterior enterocœls retain the position of the primary pair of peritoneal vesicles, and one of them (the left) opens to the exterior at its posterior end by means of the water-pore. Besides these there is formed somewhat later a hydrocœl, lying on the left side between the anterior and posterior enterocœls, and apparently derived from the latter; at this stage it has no communication with the anterior enterocœl.

Echinids.—These have two pairs of enterocœls and a water-pore, as in Ophiurids; the hydrocœl occupies the same position as in that group, but appears to arise from the anterior enterocœl, and to retain its communication with it.

Asterids.—The anterior and posterior enterocœls are distinguishable on both sides, but are not usually separated, though they are so on the left side in one form. The water-pore and hydrocœl occupy their usual positions, but the latter remains open to the anterior enterocœl, from which it probably arises.

Crinoids.—Only one anterior enterocœl is present. The hydrocœl is at first connected with this anterior enterocœl, but subsequently becomes independent. The water-pore opens to the anterior enterocœl, and a pair of posterior enterocœls lie beside the stomach.

Holothurians.—The left anterior enterocœl appears to be present, but rudimentary, and connected from the first with the hydrocœl. Two posterior enterocœls exist as in other groups.

From these facts we may arrive at the following conclusions:

(1) A pair of anterior enterocœls was probably originally present in all Echinoderms. So long as the left anterior enterocœl of Ophiurids and Echinids was confused with the hydrocœl, doubts were frequently expressed as to whether it ever had a fellow on the right side (**4**, p. 458; **11**, p. 609; **17**, p. 141; **26**, p. 49); and even when this was admitted to exist, it was hinted that this bilaterally symmetrical arrangement might be pathological (**17**, p. 142). However plausible this supposition may formerly have seemed, it appears to me absolutely untenable in the face of the new evidence here advanced. Pathology may account for such obviously monstrous forms as that observed by Metschnikoff (**19**, p. 64), but the term is clearly inapplicable to a condition which obtains with the utmost regularity in every individual member of two groups (Ophiurids and Echinids). Nor is it any more satis factory to assume that a portion of the enterocœl is cut off on the right side merely for the sake of symmetry (**26**, p. 50) and is then allowed to atrophy without further development. The only tenable view, as it seems to me, involving a secondary origin for these anterior enterocœls, is that they are derived by a species of segmentation from such a condition as is found in many Asterids, in which the œsophageal and gastral sections of the cœlom are continuous on each side of the body; but the apparently primitive character of the Bipinnaria, in which the

anterior and posterior enterocœls of the left side are distinct, is, as already remarked, opposed to the idea that the other Asterids are primitive in this respect. If union of the cavities originally obtained (as is not improbable), there is strong reason for supposing that before the separation of the existing groups of Echinoderms, the segmentation of each lateral cavity into an anterior and a posterior part had already occurred.

(2) The hydrocœl is generally formed distinctly later than the other cavities; indeed, the only apparent exception to this is afforded by the Holothurians, and in these it is quite as reasonable to consider the anterior vesicle to be an anterior enterocœl as to follow previous writers in regarding it as the hydrocœl. This being so, it seems probable that the hydrocœl is of later phylogenetic origin than the enterocœls. The entire absence of any trace of a right hydrocœl makes it improbable that this organ was ever paired; but we must not lay too much stress on this evidence, seeing that in Holothurians and Crinoids the right anterior enterocœl has entirely disappeared. In its mode of origin the hydrocœl varies, but its normal position, when formed, seems to be between the anterior and posterior enterocœls, not separated by either of them from the wall of the stomach.

(3) The water-pore always (with the possible exception of Holothurians) arises in connection with the posterior end of the left anterior enterocœl, and only communicates indirectly, if at all, with the hydrocœl. In all pelagic larvæ it appears exceedingly early—probably always before the hydrocœl (except, perhaps, in Holothurians). In Asterina, on the other hand, it is formed later, simultaneously with the hydrocœl; while in Antedon it does not make its appearance till after the hydrocœl has become five-lobed, and the larva has escaped from the vitelline membrane. It might be thought from this that the water-pore was really a late development, which had become precociously formed in pelagic larvæ on account of its physiological importance, and that its real time of formation was about the same as, or later than, that of the hydrocœl. This

may be so, but the evidence seems to me to point rather to the water-pore having existed in a very early stage in the history of Echinoderms, probably before the hydrocœl had arisen.

A word must be said here as to the probable function of the water-pore. Bearing in mind Hartog's experiments and remarks (12) upon the madreporite of the adult, I carefully observed not only the apparent motion of the cilia but also the action of the currents produced by them, as indicated by the motion of particles suspended in the water. The apparent motion of the cilia was inwards, which, as we know, indicates that the real current produced is exhalent. If we need an illustration of this we have only to turn from the water-pore to the œsophagus, and observe the motion there; for in this case, while the apparent motion is outwards, particles suspended in the water show clearly that the current passes inwards. With regard to the water-pore also particles suspended in the water will guide us as to the direction of the current, though not so readily as in the case of the œsophagus. No particles were ever observed to pass in through the pore, though there was nothing in their size to prevent them; on the other hand, it was difficult to observe an exhalent current owing to the rapid motion imparted to the particles by the external cilia of the larvæ; nevertheless, in a few cases in Echinid Plutei, in Bipinnaria, in Auricularia, and in Tornaria, a definite repulsion of particles from the pore was noticed. Taking this in connection with the apparent motion of the cilia (also observed in Ophiurid Plutei) it seems safe to assert that the current passing through the water-pore is an exhalent one, though, from the very slight disturbances produced by it in the surrounding water, I conclude that it is not usually very strong. It is, of course, not proved that the current is never inhalent; but until such a reversal of its direction has been definitely observed we have no particular reason for supposing that it ever occurs.

As many of the larvæ observed by me had as yet no hydrocœl, we arrive at the conclusion that in Echinoderms as well as in

Balanoglossus the water-pore and the short tube by which it communicates with the enterocœl represent a primitive nephridium. It would seem from Hartog's observations that in the adult the nephridial function is transferred to the water-vascular system.

The existence of a pair of anterior enterocœls in Echinoderms is to some extent opposed to the homology which I formerly attempted to establish between the anterior enterocœl of Antedon and that of the larva of Balanoglossus. It is true that the existence of two pores belonging to the anterior cavity in the larva of B. Kupfferi (**30**) is evidence of the paired nature of this cavity; but, on the other hand, two distinct anterior cavities are never, so far as I know, present in Balanoglossus, while no instance is yet known in which a pore normally occurs in connection with the right anterior enterocœl of Echinoderms. The present paper, therefore, adduces no new evidence in favour of the phylogenetic connection of the Echinodermata and Enteropneusta, though it does not seriously weaken the probability of such a connection.

II. Further Development of Hydrocœl: Water-Tube.

Ophiurids.—We left the hydrocœl of this group as a closed elongated vesicle stretching forwards for some distance under the anterior enterocœl, and backwards as far as the posterior enterocœl. The next change consists in the formation of five lobes on its outer (left) border. This has been already described by previous observers, and need not be dwelt upon here; it is only necessary to add that the water-pore usually lies at first nearly at the level of the third lobe, but by a further shifting forwards of the hydrocœl it afterwards comes to lie over the interval between the fourth and fifth, or even over the fifth (posterior) lobe itself. When this stage has been reached we notice the first formation of the water-tube (= stone-canal), which arises as an outgrowth of the posterior end of the hydrocœl, between the fourth and fifth pouches, and has, like the rest of the hydrocœl, a columnar ciliated epithelium. It runs directly dorsalwards, and after an extremely short course, opens into the comparatively thin-walled anterior enterocœl almost immediately below the pore. From the fact that it is almost impossible to get anything but a directly dorsal or directly ventral view of a living Ophiurid Pluteus, the relations of the parts just described are not always easy to make out; and owing to the extreme minuteness of the cavities concerned, sections are even less satisfactory than the living objects. Nevertheless, with favourable living specimens (Pluteus paradoxus is one of the most consistently satisfactory forms, but there is much individual variation) placed in an extremely small quantity of water, and examined with a high power (Zeiss, Obj. E or F), it is not usually a very difficult matter to see the cilia working in the water-pore at the surface, and in the up-turned mouth of the water-tube at a deeper level.

In fig. 3 I have attempted to give some idea of a dorsal view of this region of the body, but it is impossible in such a figure to convey a correct notion of the differences of level, and the arrangements of the parts will be better understood from the diagram (fig. 2).

Shortly before the final metamorphosis of the whole larva into the pentagonal form, the hydrocœl grows round the œsophagus into the form of a ring. This has been already described by Metschnikoff, but I have not found it easy from his description to tell in which direction this growth takes place, and as others may have shared my difficulty, I may be excused for adding some details to his account.

Fig. 4 gives nearly all that is necessary; the fourth and fifth lobes retain their places, while the three anterior ones grow across to the right side on the dorsal side of the œsophagus. On reaching the right side, the first lobe passes underneath (ventral to) the anterior enterocœl and the œsophagus, and so nearly joins the fifth, which at the same time bends slightly in under the œsophagus as if to meet it.

The further history of these parts cannot be described without entering into a detailed account of the metamorphosis, but it is important to notice that fig. 4 represents a stage in which the hydrocœl has already formed a ring round the œsophagus with five tentacular outgrowths, while the rest of the body still retains its bilateral form.

Echinids.—After the stage represented in fig. 8 the hydrocœl pushes its way farther back (not forward, as in Ophiurids) until it comes to lie in the centre of the left side. In doing this it does not pass on the outside of the posterior enterocœl, but lies close to the wall of the stomach, while the posterior enterocœl forms a kind of horse-shoe round it, as represented in fig. 7.

In this figure the hydrocœl already possesses five lobes, and is itself curved into the form of a ring, incomplete towards the posterior end. The tube connecting it with the anterior enterocœl is now much longer than before, and has acquired a columnar epithelium; it is, as already mentioned, the water-tube (= stone-canal), and enters the hydrocœl ring anteriorly and slightly dorsally. Shortly after this the hydrocœl ring closes completely, leaving a central perforation (**19**) through which, at a much later period, the œsophagus grows.

We must now return to the anterior enterocœl. It has usually been stated (**1**, p. 714; **18**, p. 42; **14**, p. 40; **9**, p. 137) that the water-tube (= stone-canal) opens directly to the exterior by the water-pore, the hydrocœl being supposed to be formed either by a direct metamorphosis of the left œsophageal enterocœl (**1** and **18**), or as an outgrowth from the left posterior enterocœl (**11**, p. 609; **17**, p. 141; **26**, p. 49), but in his last note on the subject (**19**) Metschnikoff tells us that, though most of the cavity by the œsophagus goes to form the hydrocœl, a considerable portion forms a pulsating vesicle into which the pore at first opens. It might be supposed that this pulsating vesicle was the anterior enterocœl of my account, but this does not appear to me to be the case.

In fig. 9 I have given a view of the pore and its surroundings so far as I have been able to make them out. On the left is seen the water-tube (= stone-canal) coming up from the hydrocœl, and opening into a swollen portion of the anterior enterocœl, which I have marked "ampulla," and this in its turn opens to the exterior by a conspicuous median pore. Also in the median line, and partly hidden by the pore, is a large pulsating vesicle, which is doubtless the same as that seen by Metschnikoff; it is overlaid by a reticulated calcareous plate (not represented), which surrounds the pore, and makes it extremely difficult to determine the relations of the subjacent parts. That the pore does not open directly into the pulsating vesicle I am almost certain, while I have seen its opening into the non-contractile ampulla in a large number of specimens. It is certainly, however, possible that there may exist a communication between the ampulla and the pulsating vesicle which has escaped my notice; the wall separating them is undoubtedly very thin, and a small valvular aperture in it would be exceedingly hard to see in the living animal, while it would be practically impossible to detect in sections. I have not as yet been successful in tracing the origin of this pulsating vesicle, but, as far as I can make out, it is at first more widely separated from the anterior enterocœl than in the stage figured, and I have no reason to think that it is derived from this enterocœl; I am more disposed to believe that it is of schizocœl origin, and that it is at no time connected either with the water-pore or the ampulla.

Most of the parts represented in fig. 9 are subject to considerable variation in size, not only in different forms of Plutei, but even in Plutei belonging to the same species; it may, however, be stated generally that the right anterior enterocœl and the anterior continuation of the left anterior enterocœl (i. e. all except the ampulla) are difficult to see in the living animal, since they lie rather under the œsophagus, though they are easily visible in sections. In the specimen figured the water-tube (stone-canal) and the thick-walled tube from the water-pore (pore-canal) are continuous on one side; but in some other Plutei, and especially in Spatangids, they are more or less widely separated; in fact Fewkes (9) has evidently seen only the water-tube, and has described its opening into the anterior enterocœl as the water-pore; the real water-pore is always median or even somewhat to the right, except in the very earliest stages, but it is certainly not easy to see in the opaque Spatangid Plutei. What Fewkes describes as a movement of the pore is a growth of the water-tube (stone-canal) to join the pore-canal.

Asterids.—In this group the primary opening of the hydrocœl into the anterior enterocœl continues to exist after the former has acquired its five primary tentacular lobes; but it does not, as in Echinids, give rise directly to the water-tube. The latter arises after the appearance of the tentacular pouches, and in the small Bipinnaria above described, in which the anterior and posterior enterocœl are distinct, runs close to the surface of the stomach in the mesentery separating these two cavities, and opens into the anterior enterocœl beside the water-pore: it occupies a corresponding position in other Bipinnariæ and in Asterina, in which the mesentery in question is incomplete.

Not only is the primary connection of the hydrocœl with the anterior enterocœl distinct from the water-tube, but they are in different interradii; this has been proved by Ludwig for Asterina, and is apparently true also of Bipinnaria, though I cannot assert this with any confidence.

Crinoids.—The hydrocœl forms a ring (long, incomplete) through which the œsophagus grows. The water-tube (stone-canal) starts from one end of this incomplete ring, and opens into the anterior enterocœl (7, p. 21). It is, of course, impossible to say whether this new opening is in the same position as the primary one, since the latter is closed before the formation of the tentacular lobes.

Holothurians.—In Auricularia the primary opening between the anterior enterocœl and the hydrocœl persists as the water-tube (stone-canal), but instead of remaining short, as in figs. 22 and 24, it elongates rapidly just before metamorphosis into the "Pupa," and forms a tube with columnar epithelium. At the same time the cells forming the wall of the anterior enterocœl become rounded and increase in number, at the expense of the cavity, so as to form a bunch of cells, which

Metschnikoff (**18**, pl. iii, fig. 20), at a later stage, described as mesodermic; it is really present in the oldest Auriculariæ, though in these it escaped the notice of Metschnikoff and of Semon (**28**). In fig. 25 I have represented part of a section through a larva just entering into the pupa stage, in which the opening of the water-tube into the anterior enterocœl is clearly seen. This section is also useful as illustrating the various parts into which the tube, usually spoken of as the "stone-canal," stretching from the water-vascular ring (hydrocœl) to the water-pore, is divisible; (1) water-tube (= stone-canal of Asterid), (2) anterior enterocœl, and (3) pore-canal; these three parts are distinguishable in all Echinoderm larvæ, though the second has been frequently overlooked, and the first and third consequently spoken of as one.

The remnant of the anterior enterocœl is also traceable in Cucumaria (fig. 26), though I have not yet followed its development. In the series of sections from which this figure is taken the water-tube and pore-canal are cut transversely; the columnar epithelium on one side of the cavity in the section figured, is continuous with those of the pore-canal and water-tube, which appear respectively in sections above and below this. The same continuity of epithelia is seen in Synapta (fig. 25) in some Echinid Plutei (fig. 9), and in Asterina (**17**, fig. 72).

Shortly before the metamorphosis of Auricularia into the pupa the hydrocœl sends out five pouches (primary tentacles), and almost immediately afterwards six smaller ones (alternating with the former), five of which become the five longitudinal water-vessels, while the sixth becomes the primary Polian vesicle. The growth of the hydrocœl into a ring accompanies metamorphosis.

There is some difficulty in determining the position of the water-tube in relation to the closing point of the water-vascular ring. Semon (**28**, p. 196) states that it lies opposite one of the smaller pouches (longitudinal water-vessels), and on this he bases his determination that these longitudinal vessels are interradial, and that the five primary tentacles are radial, and homologous with the five primary tentacles of other Echinoderms. His evidence seems to me insufficient; on p. 197 he refers to pl. viii, fig. 3, as proving the interradial position of the longitudinal vessels; yet in this figure the water-tube (stone-canal) is distinctly adradial, i. e. between a tentacle and a longitudinal vessel, and no figure whatever is given of a stage (supposed to precede this) in which the water-tube is midway between two tentacles. For my own part I have never seen such a stage as this, but have always found the water-tube to be adradial from the first, though I do not agree with Semon as to which adradius it occupies.

In fig. 27 I have given the result of my observations in a diagrammatic form comparable to Semon's fig. 3 (pl. viii): it will be seen that in my figure we have to cross two primary tentacles and one longitudinal vessel in passing from the water-tube to the Polian vesicle; now, according to one of Semon's figures (fig. 3), we have to pass two primary tentacles and two longitudinal vessels; but another of his figures (pl. viii, fig. 2), when carefully examined, gives the same results as mine; and the same position is assigned to the water-tube in Baur's figures (**6**). Whatever doubts may exist on this point after the examination of Auricularia are easily set at rest by sections through young Synaptæ, for in these it is no difficult matter to ascertain the positions of the water-tube and Polian vesicle, while the primary tentacles and longitudinal vessels are exceedingly conspicuous. It is surprising that Semon did not adopt this method of inquiry, which would also have set at rest his doubts (**28**, p. 305) as to which end of the hydrocœl formed the Polian vesicle.

SUMMARY AND CONCLUSIONS.

We will now summarize the facts above related, and see what conclusions can be drawn from them as to the nature and origin of the hydrocœl; in doing so we shall repeat for the sake of clearness some of the arguments used on p. 420.

(1) Origin.—The hydrocœl always arises on the left side as a derivative of one or other division of the cœlom.

In Ophiurids it is formed from the posterior enterocœl.

In Echinids probably from the anterior enterocœl.

In Asterids (Bipinnaria) from the anterior enterocœl; the case of Asterina is easily reducible to this.

In Crinoids it and the anterior enterocœl come off together from the gut, and then separate.

In Holothurians it and the anterior enterocœl are not at first distinguishable from one another, and are always connected.

From the fact that in the first three groups there is a period in which the hydrocœl does not yet exist, though the anterior enterocœl is already formed, we may assume that the former is of later phylogenetic origin; so that in Crinoids and Holothurians, where the two cavities arise together, the hydrocœl may be regarded as a derivative of the anterior enterocœl. The frequency with which this origin of the hydrocœl occurs in ontogeny might seem to indicate that it was of phylogenetic significance, but it is not easy to see why, if so, there should be any departure from this condition in Ophiurids, which, in possessing two well-developed anterior enterocœls, seem somewhat primitive. On the other hand, the variation in the ontogeny of the hydrocœl may mean that when it originally appeared the anterior and posterior enterocœls were connected, as they are in Asterina and some Bipinnariæ, and that in separating them the other groups have adopted different methods of producing the hydrocœl; but the fact that the Bipinnaria in which these two divisions of the cœlom are separated is in other respects primitive, is opposed to this view. A slightly more satisfactory result is arrived at by regarding the condition found in Ophiurids as primitive. Then we must assume that, on account of its physiological importance to the free-swimming larva, an opening was formed at an early stage into the anterior enterocœl (before the water-tube could arise), and that this in time gave rise to the ontogenetic derivation of the hydrocœl from the anterior enterocœl, such as we find in all forms except Ophiurids. The fact that this communication is not kept open in Crinoids till the formation of the water-tube, might be explained by their having comparatively recently acquired a large amount of food-yolk, and passing a very short free-swimming existence. But this is merely a suggestion, and it is difficult to understand why the pelagic larvæ of Ophiurids should have been able to do without the early connection of the hydrocœl with the anterior enterocœl, supposed to be of such importance to other larvæ; or why this connection should not have been made to coincide with the water-tube (stone-canal) in Asterids as it does in Echinids and Holothurians. Possibly the true explanation is, that the hydrocœl originally arose in some more complicated way, which has since been simplified, independently, by each of the different groups, and is no longer repeated in the ontogeny of any one of them.

(2) Connection with the Anterior Enterocœl.—The hydrocœl never has an external pore of its own, but always at some time opens into the anterior enterocœl, and so forms an indirect communication with the exterior; there are two ways in which this communication may be established:

(A) In those cases in which the hydrocœl is derived from the anterior enterocœl, there is, of course, a communication from the first.

(B) At some period or other, but usually late, a water-tube (stone-canal) is formed as an outgrowth from the hydrocœl; it has a columnar ciliated epithelium.

These communications (A and B) coincide in Holothurians, and probably in Echinids; but even in these groups the formation of a definite columnar epithelium in the water-tube occurs somewhat late—after the appearance of the primary tentacles in Holothurians (compare figs. 7 and 27).

In Asterids the two communications coexist but do not coincide, being in different interradii. The water-tube is formed after the pouching of the hydrocœl.

In Crinoids (Antedon) the primary communication (A) closes too early for its exact position to be determined. The water-tube appears after the primary tentacles.

In Ophiurids the connection (A) never exists at all

The water-tube is formed after the hydrocœl has become lobed.

These facts seem to show that even if the derivation of the hydrocœl from the anterior enterocœl is of phylogenetic significance, there must have been a subsequent time when the two cavities were entirely separated, otherwise it is difficult to understand why the primary communication does not always coincide with the water-tube, as it does in Holothurians and Echinids, but is sometimes so far distinct from it as to be in a different interradius (Asterids). It seems more rational to regard the condition found in the two former groups as secondary (perhaps as a physiological hastening of the connection between the hydrocœl and the exterior), and to suppose that the water-tube is a secondary structure belonging to a comparatively late stage in the phylogeny of Echinoderms.

(3) Closure of Water-vascular Ring.—Ludwig (**14**, p. 45) has already alluded to the variation in the point of closure of the water-vascular ring with regard to the position of the water-tube (stone-canal); but as I have been able to collect some data which he did not possess, it will be well to review the whole matter with some care, and for this purpose it seems to me that the diagram (fig. 28) will be of more use than the most detailed description of the facts. For reasons which will be given later the interradius of the water-tube is placed anteriorly; the anterior part of the water-vascular ring lies on the dorsal side of the œsophagus, while the posterior part lies beneath it. The positions marked for the closure of the water-vascular ring rest principally on my own observations, but that of Asterina is given on Ludwig's authority, while that of Ophiurids has been already described by Metschnikoff, whose account I can confirm. Barrois's account for Antedon differs from mine in that he puts the point of closure on the other side of the water-tube, though in the same interradius (**5**, p. 608). The case of Holothurians cannot be settled till we know whether the radii are marked by the primary tentacles (Holoth., I), or by the longitudinal vessels (Holoth., II).

Bipinnaria has not been very satisfactorily studied, and it is not yet certain whether in it the hydrocœl ever forms a horseshoe curve shut off from the anterior enterocœl, as it does in Asterina, or whether the new œsophagus simply grows through it and perforates it as Metschnikoff asserts (**18** and **19**).

All this variation is certainly very puzzling; but if, as seems to me necessary, we regard the interradius of the water-tube as a fixed point, we are almost bound to conclude that the present position of closure of the water-vascular ring is secondary, at any rate in most groups. We have already seen reason to doubt whether the derivation of the hydrocœl from the anterior enterocœl, which obtains in the ontogeny of most groups, is really phylogenetic, and we are now tempted to ask whether the whole development of the hydrocœl, up to the time when it forms a complete ring round the œsophagus (the earliest stage in which all Echinoderms agree), has not undergone secondary changes which completely mask its true phylogenetic history. It is to be hoped that further investigations may throw some more light on this point, which at present forms one of the most insoluble, as well as the most important, questions in Echinoderm morphology.

III. The Skeleton.

The greater part of the development of the skeleton belongs to the pentagonal stage, and with this we are not at present concerned; nor need we mention the purely larval skeletons of Ophiurid and Echinid Plutei—only such parts of the permanent skeleton as are developed in the Dipleurula will be considered here.

Ophiurids.—No satisfactory observations have hitherto been made on the first appearance of the skeleton in this group. Ludwig (**16**), in his valuable studies on the skeleton of Amphiura, found that the radials and terminals were present before any other plates of the aboral surface, but he was unable to determine which of these sets was the first to appear. Fewkes (**10**), working on the same animal, states positively (p. 139) that the radials appear before the terminals, though he admits that this statement rests only on the relatively small size of the terminals in the young pentagonal embryo. On p. 132 he further states that the first and second adambulacral plates appear before the terminals, but probably after the radials. I have myself worked out the first appearance of these plates in Amphiura squamata, and am convinced that the plates in the bilateral stage, which Fewkes took for the adambulacrals (10, p. 131, figs. 7, 8, and 10), are really terminals; but as the whole subject is far more easily studied in the various forms of Plutei, I shall begin with a description of these.

Soon after the formation of the water-tube (stone-canal), and shortly before metamorphosis, ten skeletal plates make their appearance simultaneously in the mesoderm surrounding the posterior enterocœls; five plates accompany each cavity, and are arranged along it in a straight line antero-posteriorly, three being dorsal and two ventral, as shown for the left side in the diagram (fig. 2); it will be convenient to state at once that those on the right side are the radials, and those on the left the terminals. In some few cases the terminals appeared before the radials, and several times the dorsal plates of both series appeared before the ventral. It is possible that these peculiarities may be constant for certain forms of Plutei, but of this I have not sufficient evidence. Sometimes simultaneously with, but usually some hours later than, the radials and terminals a plate appears in the middle of the right side, which is destined to form the dorso-central. Later again than this there arises another plate on the left side, just in front of the water-pore; it is the madreporic plate, or first oral (fig. 3). These twelve plates are all that were ever observed in the bilateral larva. It is not until after metamorphosis has commenced that the adambulacral plates make their appearance.

The development of the plates in Amphiura squamata so closely resembles that already described, that the details of it will be postponed to a future paper. The opacity of this larva, the excessive development of the larval skeleton, and certain irregularities to which its skeleton seems peculiarly liable, render it a far more troublesome object for study than the transparent Plutei.

It is not my intention in the present paper to enter into a detailed account of the metamorphosis of the Pluteus into a pentagonal Ophiurid, but it will be well to give a few facts in support of the statement that the terminals are developed round the left enterocœl. In fig. 4 we see that the rapid growth of the right and left enterocœls to meet one another in the middle dorsal line, has caused the formerly longitudinal series of plates to become more or less bowed, and the dorso-central to appear distinctly on the dorsal surface of the larva. At the same time or rather later, the terminals assume a peculiar form (see **18**, pl. vi, fig. 11, p^1—p^3), and over each of them is developed a marked thickening of the ectoderm. Without pausing to describe the next stages we will at once pass on to a much later one, represented in fig. 5. The whole of the right enterocœl has shifted so far onto the previously dorsal face of the larva that the fourth and fifth radials (counting from before backwards, as in fig. 2) are visible from the dorsal side. In correspondence with this the left enterocœl is passing round towards the ventral surface, so that the three dorsal terminals lie close to the left margin. Besides this there has occurred a great shortening of the anterior region of the larva, and the most anterior terminal has shifted forwards and across towards the right, so that it now forms the anterior median point of the body of the larva (compare **23**, pl. iii, figs. 1, 3, and $4 f^1$). The hydrocœl, too, has undergone great changes, which cannot be fully described here, but a comparison of figs. 4 and 5 will give some indication of them: it will be noticed that in the latter the madreporic plate has shifted its position, and lies anteriorly and to the right, hence it will be easily understood that that tentacular pouch, which formerly (fig. 2) lay just behind the water-tube, now lies at the anterior end of the body, immediately under the anterior terminal; while that pouch, which was the most anterior in fig. 2, and is on the right in fig. 4, now (fig. 2), lies under the second terminal plate, by which its extremity ("unpaired tentacle") is about to be embraced. Between the first and second terminals, the second adambulacral plates are now visible; the first pair belonging to this interradius, and both pairs of other interradii lie at too deep a level to be shown in this drawing.

If my description has been followed up to this point, it will be an easy matter to follow the plates, which I have identified as the radials and terminals, into the stage represented in fig. 6, and the correctness of the identification will then have been sufficiently proved.

Asterids.—In the small Bipinnaria seen in fig. 14 the five terminal plates are already present, though the lobes of the hydrocœl are not yet developed. In Asterina, however, the primary tentacles are formed before any skeletal plates appear, and certain plates in connection with the water-vascular ring appear as early as, if not earlier than, the terminals. These, however, need not detain us now.

Fig. 14 shows clearly that the terminals are developed round the left enterocœl, as in Ophiurids, and I have supplemented this view of the whole larva by sections through this and another form of Bipinnaria (B. asterigera), in both of which this relation of the plates to the enterocœl was quite evident. The case of Asterina, which offers some difficulties, will be considered presently.

Up to the present time it has, I believe, been invariably assumed that the terminals of Asterids and Ophiurids belonged to the right enterocœl. No attempt, so far as I know, has been made to prove this for the latter group, but for Asterids we have the authority of Agassiz (2, p. 32), and it is worth while to spend a few moments in explaining how his mistake arose. At the time when he wrote, the ultimate fate of the two primary enterocœl pouches was still very imperfectly understood, and he believed that the left pouch ("left water-tube," as he calls it)[1] gave rise solely to the water-vascular

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[1] It will be noticed that Agassiz' use of the term "water-tube" is very different from that adopted in this paper. Here it is substituted for the

system, while the right pouch formed the whole of the adult body-cavity. Now, the terminal plates ("brachial plates" of his description) are undoubtedly formed to the right of the water-vessel (hydrocœl), and hence Agassiz was led to speak of them as formed round the right "water-tube" (enterocœl); and although subsequent writers must long have been aware that the left enterocœl pouch enters largely into the formation of the adult body-cavity, yet they have made no fresh investigation into the relations of the terminals. It is not a little curious that the dorsal mesentery, separating the right and left enterocœls, is actually represented in one of Agassiz' figures (**2**, pl. v, fig. 6) to the right of the terminals.

The next plate to appear is the madreporite. It arises close to, but nearer the median line than, the water-pore, which before long it embraces. In one form of Bipinnaria, which I more than once obtained, it lay in the same straight line with the terminals; but usually it is more to the right, as shown in fig. 14. In the larva from which this figure was taken the terminals only were present, but I have added the madreporite from another larva, in which it was precociously developed. It really belongs to a somewhat later stage.

Seeing that the terminals, both in Asterids and Ophiurids, belong to the left enterocœl, and not, as hitherto supposed, to the right, it obviously becomes important to reconsider the position of the madreporic plate in the two groups. This plate and the other orals of Ophiurids have always been assumed to belong to the left enterocœl, and it is, I think, practically certain that this view is correct, though the only fresh evidence I can offer of it is derived from the position of the madreporite in the bilateral larva, in which it lies over the left anterior enterocœl. The question now arises, is it not possible that the madreporite of Asterids may also belong to the left side, and not, as hitherto asserted, to the right? If this were so, the position taken up by Ludwig on other

inappropriate expression "stone-canal" (= Steinkanal = canal de sable). Agassiz applies it to the cœlom, and its derivative the hydrocœl.

grounds (**15**, p. 79), that the madreporic plates of Asterids and Ophiurids are homologous, would receive new and striking support.

Agassiz (**2**) and Götte (**11**, p. 620) both describe the basals of Asterids as formed round the right enterocœl, but as the value of their testimony is in some degree weakened by their mistake with regard to the terminals, it will be well to give some further evidence; without, therefore, referring to the numerous arguments to which Ludwig's suggestion has given rise, I shall give the result of my own observations on Bipinnaria and Asterina. In the former most of the basals are formed late, and I have not obtained specimens which show their position satisfactorily. At first sight the case above mentioned, in which the madreporite and terminals are all in the same straight line, seems to indicate that the former also belongs to the left side; but on cutting sections we find that it does not lie over the enterocœl, but over another cavity which has not been noticed by previous observers; this cavity is situated in the median line, and is utterly unconnected with the enterocœl in any stage in which I have observed it; and though I have not with certainty traced its formation, I believe it to be of schizocœl origin, like the similarly situated "pulsating vesicle" in Echinids; it is, however, not contractile, but contains a few corpuscles which are kept in movement by cilia on the walls of the sac; it is most probably the rudiment of the blood-vascular system, but I cannot at present assert this positively.

Since nothing could be determined as to the position of the basals from such a larva as this, I next turned my attention to Asterina gibbosa, in which, as Ludwig had already made known, all five basals (including the madreporite) appear at an early period. Here, however, I met with an unexpected difficulty, for it was soon evident that my larvæ (obtained at Naples in May, 1888) did not at all agree in their internal anatomy with Ludwig's description. I must therefore, for the present, ignore his account (accepting only such parts as relate to the external form, and to the position and nomenclature of the plates[1]), and briefly describe what I find in larvæ of the seventh and eighth days of development. Fig. 17 is a partly diagrammatic view of such a larva from the dorsal (and partly left) side, the larval organ being considered anterior, and the larval mouth ventral. An oblique mesentery, separating two cavities, runs across the posterior part of the stomach, and on the left side of it are seen the three dorsal terminals (compare fig. 14), while on the right are three basals, the most anterior being the madreporite. The cavity on the left is identified from Ludwig's description as the left enterocœl, and this is supported by its relations to the terminals; but the right cavity is not mentioned by Ludwig. According to his description it too should be part of the left enterocœl, and he recognises no mesentery in the position here represented. To confirm this view of the whole animal, and to determine the relations of this right cavity, I have cut a number of transverse and longitudinal sections, and in every case the same result is obtained. This cavity is entirely shut off from that of the larval organ, and, indeed, from every other cavity; it begins a little behind the water-pore, and runs back to the extreme posterior end of the larva, being separated from the rest of the enterocœl by a ventral mesentery, as well as by the dorsal one here represented; it is correctly shown in transverse section by Ludwig (17, pl. ii, fig. 37) as a comparatively small cavity exactly opposite to the hydrocœl, but there is nothing in his description which will enable us to understand how it gets there. I have represented it again diagrammatically in fig. 16, in which is shown its relation to the dorso-central and basal plates, and the close parallelism of the terminals to the mesentery enclosing it. I have not yet fully traced its origin or subsequent fate, and until I have done so I am unable to determine its true character, or to point out the full extent of the difference between Ludwig's account and mine; but, bearing in mind the posi-

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[1] This statement requires modification: the madreporic plate is called by Ludwig the fifth basal, the one immediately behind it being the fourth, and so on. I begin with the madreporite and count backwards, as in the case of the terminals (fig. 13).

tion of the terminals in Bipinnaria (figs. 13 and 14), and that of the dorso-central in Ophiurid Plutei (figs. 4 and 5), we can, I think, have little hesitation in identifying the cavity on the right of the mesentery in fig. 17 as the right posterior enterocœl. In any case it is quite certain that the basals are not related to the left enterocœl, as the terminals are; and I fully agree with Carpenter (**8**, p. 386) and Sladen (**29**, p. 37), that this affords the strongest possible argument against the homology of madreporic plate of Ophiurids with that of Asterids, which Ludwig has attempted to establish.

Crinoids.—Here again, as originally pointed out by Götte (**11**, p. 395), whose account I can fully confirm, we find a bilateral arrangement of the primary skeletal plates, corresponding to the bilateral division of the enterocœl; that is to say, five orals are developed round the left enterocœl, and five basals round the right enterocœl. The water-pore is at first unconnected with any plate, but after a while becomes surrounded by one of the orals. In his paper on Comatula, Barrois (**5**, p. 634) gives a very different account; he begins with the statement that it is a recognised fact that in Echinids, Ophiurids, and Asterids the primary plates are developed asymmetrically, only on one side of the body. This is difficult to reconcile with the writings of Carpenter and Sladen above referred to, and is absolutely opposed to the facts related in this paper. Then, after pointing out that the plates of Antedon do not at first reach the ventral side, Barrois attempts to prove that at the time of the formation of these plates the right body-cavity is wholly dorsal, and the left wholly ventral, so that the plates belong solely to the right side. I consider this supposition to be entirely negatived by the observations of Götte and myself (**11** and **7**).

Echinids.—Although certain plates have long been known to exist in Echinid Plutei, no one, so far as I know, has traced them into connection with the plates of the young pentamerous Echinus. On the right side of an advanced Pluteus of Echinus microtuberculatus we find the plates shown in fig. 10; two of them bear pedicellariæ (the dorsal plate may have two) as well as one or two spines, the number of which varies slightly. Just anterior to the ventral pedicellaria is a third plate bearing a spine but no pedicellaria. I have ascertained, by means of sections, that these three plates lie immediately over the right enterocœl, and the relation to this cavity of the two which bear pedicellariæ is shown in fig. 20.

In one form of larva, of which I obtained but few specimens, there was also a terminal pedicellaria at the posterior end, and in Echinus microtuberculatus a small calcareous nodule, the remnant of the posterior end of one of the larval skeletal rods, occupies a similar position, and appears to develop later into a plate. On the dorsal side of a fairly young Pluteus lies a tri-radiate skeletal rod, which can be seen in fig. 8, where it is the only part of the larval skeleton represented. Later on a reticulated plate is formed round the median posterior arm of this rod, and before long envelops the water-pore, and renders the observation of the subjacent parts extremely difficult; it also possesses a spine which is seen in figs. 7 and 10. This plate is clearly the madreporite, and here, as in Asterids, we are called upon to decide whether this plate belongs to the right or left enterocœl, since it lies in a median position over what is, apparently, a schizocœl cavity. This question seems to me settled, by the fact that the five plates enumerated become the five basals (genitals) of the adult; and since three of these plates are unquestionably formed round the right enterocœl, it seems reasonable to suppose that the other two are related to the same cavity.

A comparison of figs. 10, 11, and 12 will clearly show that the five plates of the Pluteus become the basals of the adult. In fig. 11, which represents a young Echinus a few hours after its metamorphosis from the Pluteus, the plates in question have changed their positions, but are otherwise not materially altered; but in fig. 12 a much later stage is shown in which the pentamerous arrangement is more clearly marked; the number of spines and pedicellariæ, however, still remains unchanged, except that one plate has two of the latter; but this, as already mentioned, sometimes occurs in the Pluteus. A large dorso-central is also present.

Besides these five basals several other plates are formed on the left side of the Pluteus; at first I imagined that all these were related to the hydrocœl, but closer examination of them has led me to suspect that some of them should be regarded as developed round the left enterocœl; their numbers and positions are, however, extremely difficult to determine, and at present I cannot attempt to describe them. The spines belonging to some of them are shown in fig. 11.

Holothurians.—The only plates in this group which are known to be present in the bilateral larva are the "Kalkrädchen" and plates of the water-vascular ring in Auricularia, but as none of these can be homologised with plates in the other groups, it is useless to pursue the matter further at present. Our knowledge of the skeleton of other Holothurian larvæ is sadly deficient.

SUMMARY AND CONCLUSIONS.

Not only has it been shown in the foregoing pages that many skeletal plates are developed in the bilateral larva (Dipleurula), and that they bear a definite relation to the body-cavities, but the discovery that the terminals lie on the left side enables us to establish a typical bilateral form from which all the conditions found in existing larvæ may have been derived; this typical form has five radial and five interradial plates on each side, in definite relation to the body-cavities, as shown in the following Table, in which are also given the names by which the plates in question are usually known.

Position . .	Right Enterocœl.		Left Enterocœl.	
	Radial	Interradial	Radial	Interradial
Name . . .	Primary Radials	Basals	Terminals.	Orals.

In Ophiurid Plutei the ten radial plates (primary radials and terminals) and one of the orals (madreporite) are early developed; but the basals and most of the orals do not appear till the pentagonal stage is reached. In Crinoids, on the other hand, the ten interradials (basals and orals) are the first to appear, while the primary radials arise late; no terminals have yet been recognised, but now that we know where to look for them it is not impossible that they may be discovered. In Asterids the terminals are usually the first plates to show themselves, though in Asterina the basals arise simultaneously with them; in other forms the basals (except the madreporite) and the primary radials are late in appearing, and it is not yet certain whether the orals are ever developed. In Echinids the basals appear early, but we know nothing at present of the primary radials, terminals, and orals; the ocular plates have usually been identified as primary radials, but some regard them as terminals; embryology alone can decide this question, and at present my material is not sufficient for it; I am, however, strongly disposed to believe that the oculars are terminals, and that the primary radials are entirely absent.

The definite relation borne by the plates to the body-cavities is a fact of great morphological importance, and while it is absolutely opposed to Barrois's statement that all the skeletal plates of Ophiurid, Echinid, Asterid, and Crinoid larvæ are developed round the right enterocœl, it also throws considerable doubts on Semon's sweeping assertion (28, p. 282) that no homologies are to be found between the primary plates in the different groups.

Another point of considerable morphological importance receives great light from the study of the development of the calcareous plates. If we look at the lateral views of Ophiurid and Asterid larvæ (figs. 2 and 18) we shall see that the plates on each side may be regarded as forming a longitudinal series dorsal to the alimentary canal; since those plates which are apparently ventral do not reach as far forward as the anus, and may be conceived to have reached their present position in connection with a general curvature of the body. The arrangement, in fact, strongly suggests segmentation, but I cannot discuss in the present paper whether the pentamerism of the adult Echinoderms arose in this way in the skeleton, or whether it first made its appearance in the hydrocœl; the latter appears to me more probable. It is further evident from figs. 2 and 13 that, taking the terminals as marking the radii, the mouth, anus, and water-pore are at this stage all in the same interradius. It may be asked, Why should the terminals rather than the water-vascular pouches be taken to mark the radii? The fact is that during metamorphosis the hydrocœl undergoes such extraordinary changes of position that it is doubtful whether any reliance can be placed on the position of its pouches in the larva as indicating any permanent relations to the rest of the body; at any rate, it is certain that the water-pore is much more constant in its relations to the mouth and anus than to the water-vascular pouches. Thus we know that in Asterina (**17**) the most anterior tentacular pouch (in front of the water-pore) is eventually embraced by that terminal which seems to be morphologically the most posterior, i. e. the one just behind the anus in fig. 13. It is possible that this is also the case in Bipinnaria, but if so, it is the tentacular pouch alone which shifts its position; for in fig. 15 we see that, after the connection of the terminals with their respective water-vascular pouches, the mouth, anus, præoral lobe, water-pore, and water-tube still lie in one and the same interradius (see also 2 and **1**, pl. vii, fig. 6). The same figure also indicates what I shall prove more fully in a future paper, that the left anterior enterocœl becomes the so-called "Schlauchförmiger Kanal" of the adult. The Ophiurids are still more remarkable than Asterina in the behaviour of their hydrocœl; as already pointed out, the whole hydrocœl is pushed forward and round the œsophagus in such a way that the tentacular pouch immediately behind the water-tube (most posterior in fig. 2) unites with the most anterior terminal, while the pouch just in front of the water-tube unites with the terminal which is nearest the anus. In this case it is clear that to distinguish the anterior and posterior radii by means of the tentacular pouches, before they have selected, so to speak, their respective terminals, would only involve us in confusion.

In a previous paper (7, p. 294) I imagined that the arrangement found in Antedon, in which the mouth and anus are actually in the same interradius in the adult, was arrived at by a secondary shifting of the anus. This appears to be Ludwig's idea (14, p. 54), and is also advocated by Barrois for Antedon (5, p. 638). Now, however, I am compelled to regard this position of the anus as primitive, though of course it is still possible that in this particular group it may have been secondarily derived from such a condition as is found in Asterids.

Of the view here advanced, that the mouth, anus, and water-pore belong primarily to the same interradius, some further support is afforded by an examination of the Echinids. Turning to fig. 10, already described, we can without difficulty trace a series of five basal plates, beginning with the madreporite as the most anterior, working backwards by way of the dorsal pedicellaria, and ending up with the plate which bears a spine but no pedicellaria. These plates are of course interradial, but by taking the interspaces to represent the radii, we shall see that there is some reason for thinking that here again the mouth, anus, and water-pore occupy the same interradius.

Another point to be noticed is, that within this interradius the water-pore and the mouth frequently occupy adradial positions. In Ophiurids they clearly lie on opposite sides of the same interradial plate (figs. 2 and 3). The same is true of Echinids, though it is not evident from my figures; for in them too the madreporic plate is at first situated in front and to the right of the pore. In Crinoids, again, this fact is very distinct (7, fig. 45), and in these, as in Ophiurids, the adradial position of the water-pore is long marked by its excentric position in the madreporic plate.

Among Asterids I have not been able to obtain any clear evidence of this, for the madreporic plate generally seems to arise opposite the pore, and just to the right of it (fig. 14), or even slightly behind it (fig. 17). It is to be noticed that in Asterids, as well as in Echinids, the madreporic plate loses its relation to the body-cavity, which the other four basals possess, as if it were dragged out of its natural position in order to embrace the pore.

Owing to our imperfect knowledge of the development of the skeleton in Holothurians we are at present unable to trace in this group the relation of the mouth and anus to the radii.

Enough has, however, been said to make it probable that in all groups (except perhaps Holothurians) the radii of the abactinal part of the body (including the regions of the right and left posterior enterocœls) bear a very definite relation to the mouth, anus, and water-pore of the larva; that, in fact, these organs mark out an interradius which, since it contains both mouth and anus, might be called ventral, or, as it is anterior to the system of radial plates and contains the præoral lobe (where this is present), may be called anterior. The latter term seems to me preferable, since we can with less confusion apply it to the adults, though, of course, in seeking for an anterior interradius in them, we must be guided by the situation of the water-pore rather than by the indefinite and variable positions of the mouth and anus.

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EXPLANATION OF PLATES XXXVII, XXXVIII, & XXXIX,

Illustrating Mr. H. Bury's paper on "Studies in the Embryology of the Echinoderms."

Reference Letters.

Ant. Anterior. *Post.* Posterior. *Dors.* Dorsal. *Vent.* Ventral. *R.* Right. *L.* Left.

Fig. 1.—Dorsal view of a young Ophiurid Pluteus, showing the arrangement of the enterocœls and the origin of the hydrocœl. × 300.

Fig. 2.—Diagrammatic view of an Ophiurid Pluteus, from the left side.

Fig. 3.—Part of an Ophiurid Pluteus, dorsal view. × 300.

Fig. 4.—Dorsal view of an Ophiurid Pluteus, just before metamorphosis. × 180.

Fig. 5.—Dorsal view of an Ophiurid Pluteus, undergoing metamorphosis. The terminal plates are really far more complicated in their structure than is here represented. × 300.

Fig. 6.—Young Ophiurid still retaining some of the arms of the Pluteus. × 300.

Fig. 7.—Diagrammatic view of the left side of an Echinid Pluteus. × 180.

Fig. 8.—Dorsal view of an Echinid Pluteus, showing the arrangement of the enterocœls and the origin of the hydrocœl. × 180.

Fig. 9.—Part of a Pluteus of Echinus microtuberculatus, seen from the dorsal side. × 300.

Fig. 10.—Pluteus of Echinus microtuberculatus, seen from the right side. × 180.

Fig. 11.—Young Echinus microtuberculatus, a few hours after metamorphosis from the Pluteus. The calcareous plates at the bases of the marginal spines are omitted. × 180.

Fig. 12.—Plates at the aboral pole of a much older specimen of Echinus microtuberculatus (diam. ·75 mm.). × 75.

Fig. 13.—Diagrammatic view of the left side of the same larva. × 100.

Fig. 14.—Dorsal view of a Bipinnaria. × 100.

Fig. 15.—Diagrammatic view of the left side of a large Bipinnaria, the larval arms and most of the præoral lobe being cut away. Outline drawn with camera lucida. × 20.

Fig. 16.—The same, from the right side. × 100.

Fig. 17.—Larva of Asterina gibbosa on the seventh day of development, seen from the dorsal side. × 100.

Fig. 18.—Part of the left side of an Ophiurid Pluteus, seen from the dorsal side, showing the origin of the hydrocœl. × 540.

Fig. 19.—Transverse section of an older Ophiurid Pluteus, passing through the posterior part of the œsophagus. × 540.

Fig. 20.—Transverse section of a Pluteus of Echinus microtuberculatus, showing the relation of the pedicellariæ to the right body-cavity. × 180.

Fig. 21.—The same part of another abnormal Auricularia, dorsal view. × 180.

Fig. 22.—Part of an abnormal Auricularia, lateral view. × 180.

Fig. 23.—Dorsal view of the same part of a normal Auricularia. Treatment with chloral-hydrate has caused retraction of the pseudopodia of the mesoderm cells. × 180.

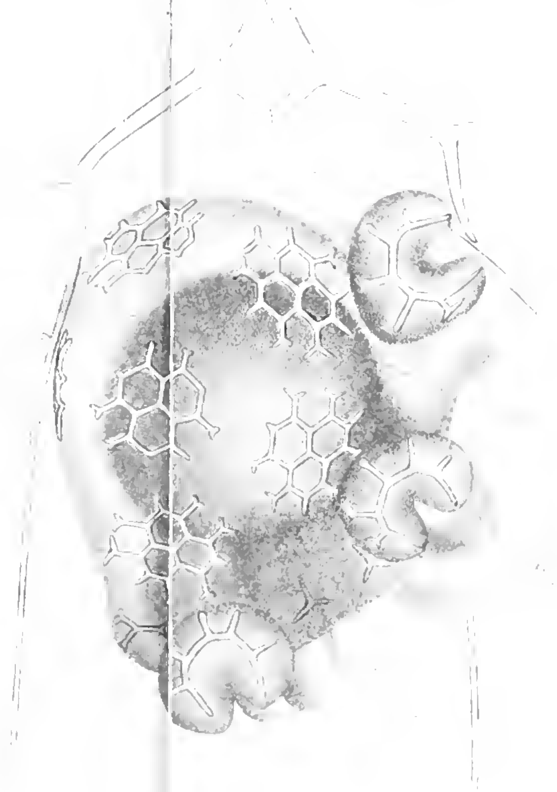
Fig. 24.—Lateral view of the same. The mesoderm cells are omitted. × 180.

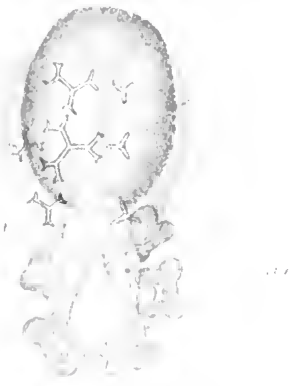
Fig. 25.—Part of a transverse section through an Auricularia, just entering into the "pupa" stage. × 300.

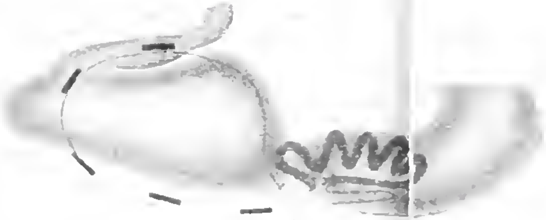
Fig. 26.—Part of a transverse section of a larva of Cucumaria Planci. × 300.

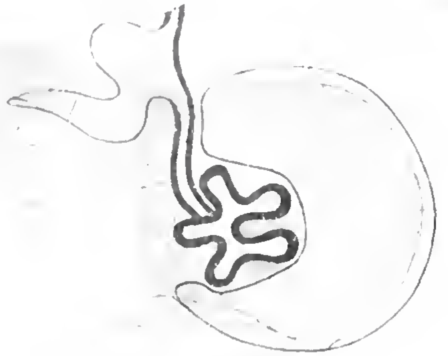
Fig. 27.—Diagram of the hydrocœl of an old Auricularia, seen from the dorsal side.

Fig. 28.—Diagram of the closure of the water-vascular ring in different groups of Echinoderms, dorsal (aboral) view.



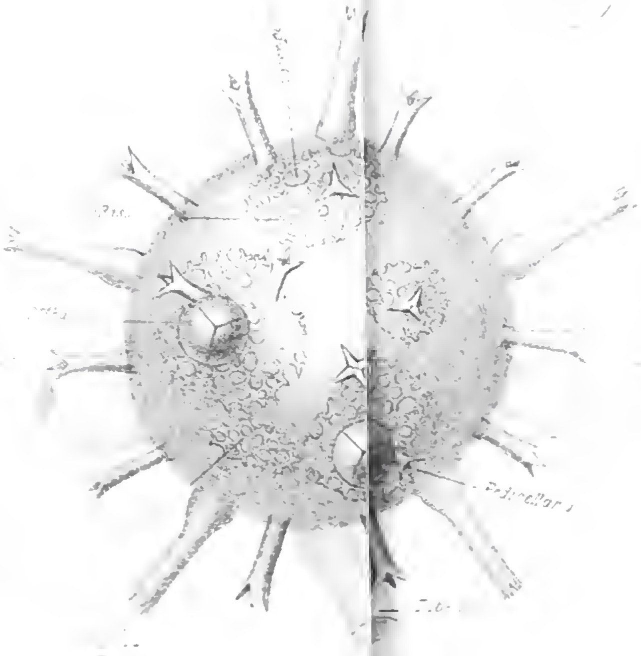


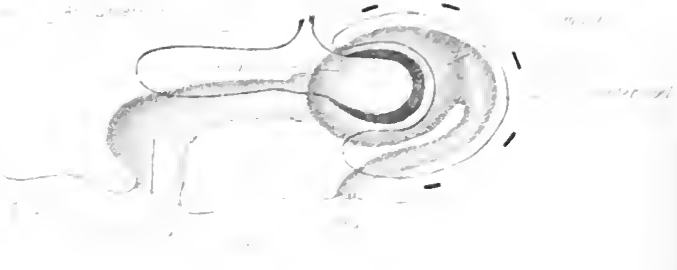


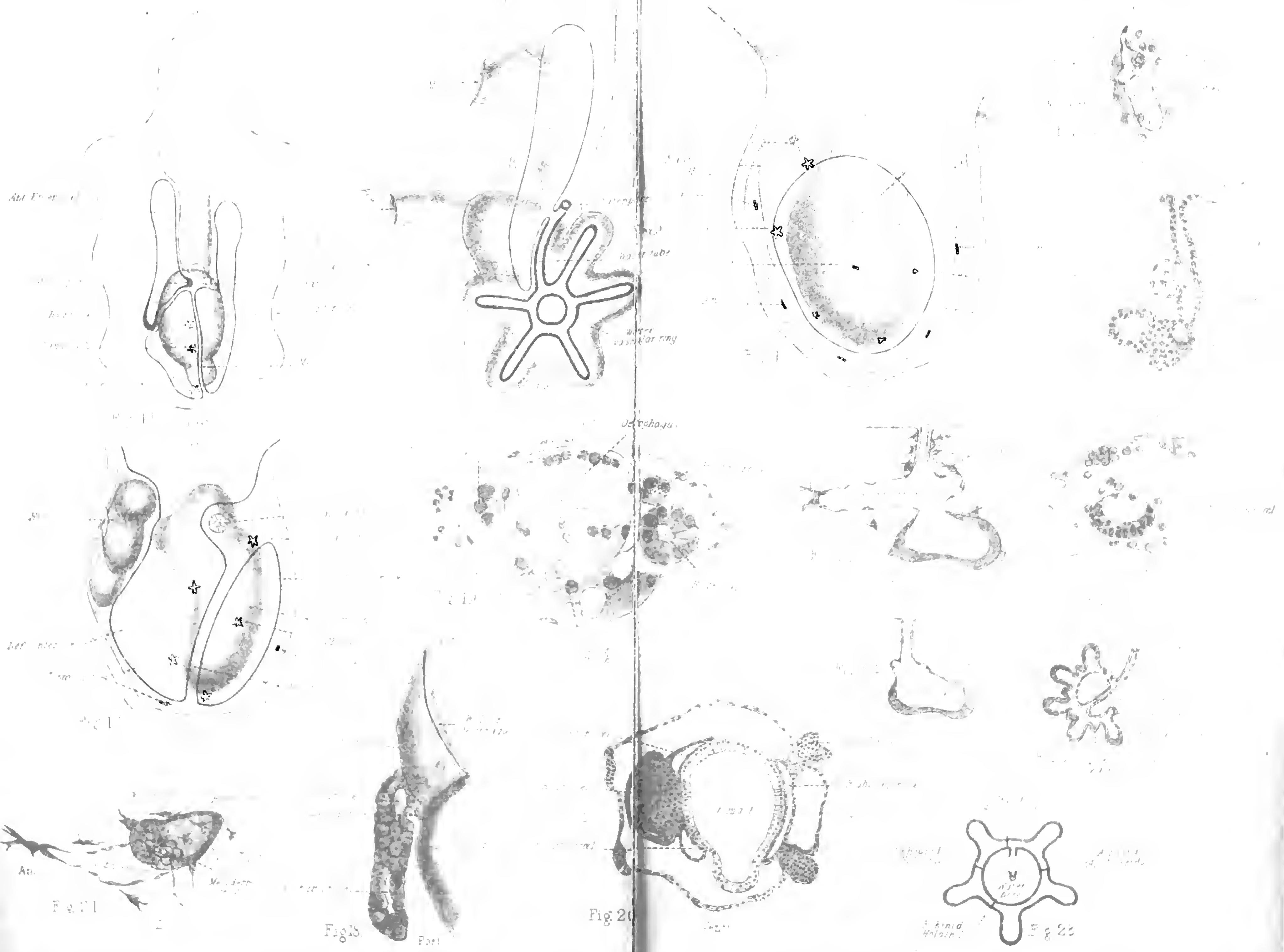



Post enteron


Fig. 10
Post


Pedicellar




water tube
water vascular ring
Oesophagus
An.
Fig 21
Fig 18
Post
Fig 20
Fig 23

Lith & Imp.

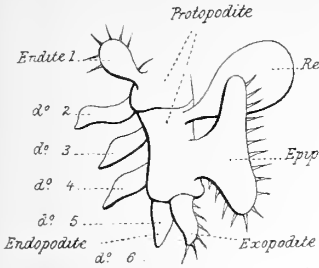


Fig. 1. Apus.

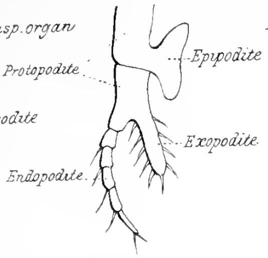


Fig. 2. Nebalia.

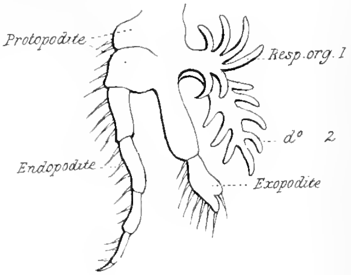


Fig. 3 Thysanopoda.

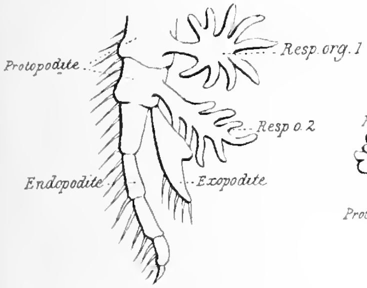


Fig. 4. Nematoscelis.

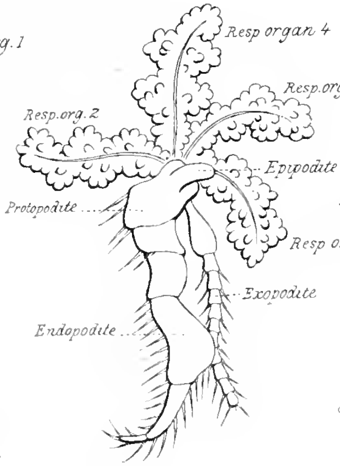
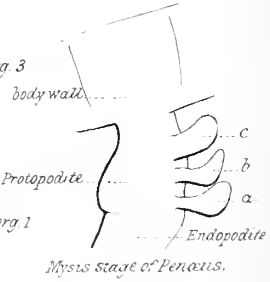


Fig. 5. Gnathophausia



Mysis stage of Penæus.

Fig. 6. Penæus Larva.

Later stage of Penæus Fig 6'

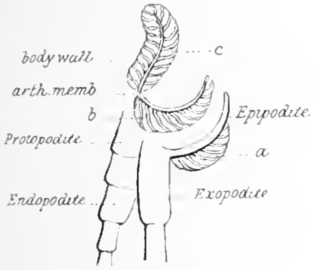


Fig. 7. Calliaxis Larva.

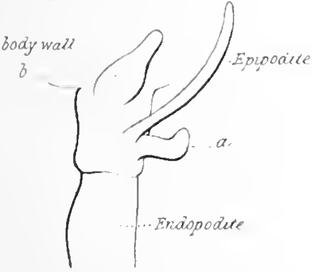


Fig. 8. Acanthocaris Larva

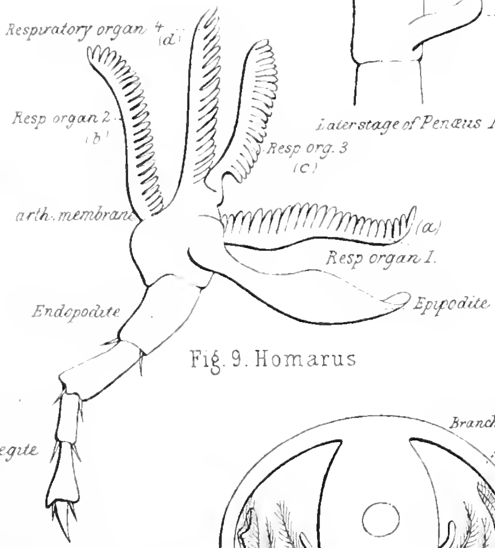


Fig. 9. Homarus

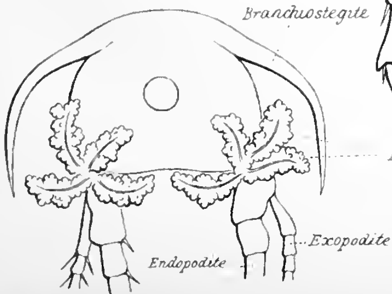


Fig. 10. Gnathophausia

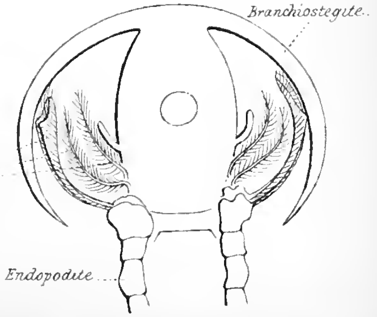


Fig. 11 Astacus.

F. Huth Lith.r Edin.r

On the Ancestral Development of the Respiratory Organs in the Decapodous Crustacea.

By

Florence Buchanan.

(A Paper read to the Biological Society of University College, London.)

With Plate XL.

In the Crayfish, so well known to all students of zoology, our attention is attracted to the varying positions of the gills, and, in reading Professor Huxley's book, especially devoted to this Crustacean, we are led to compare the different positions of these organs and their relations to each other in the different segments in many of the Decapods. In so doing the question arises as to how they have come to be situated as they are, and it is to this question that I propose, in the following paper, to attempt an answer. It must, I am afraid, be only a suggestion as to the real answer, since several details in the development of the various forms would have to be carefully worked out in order to prove the whole theory true.

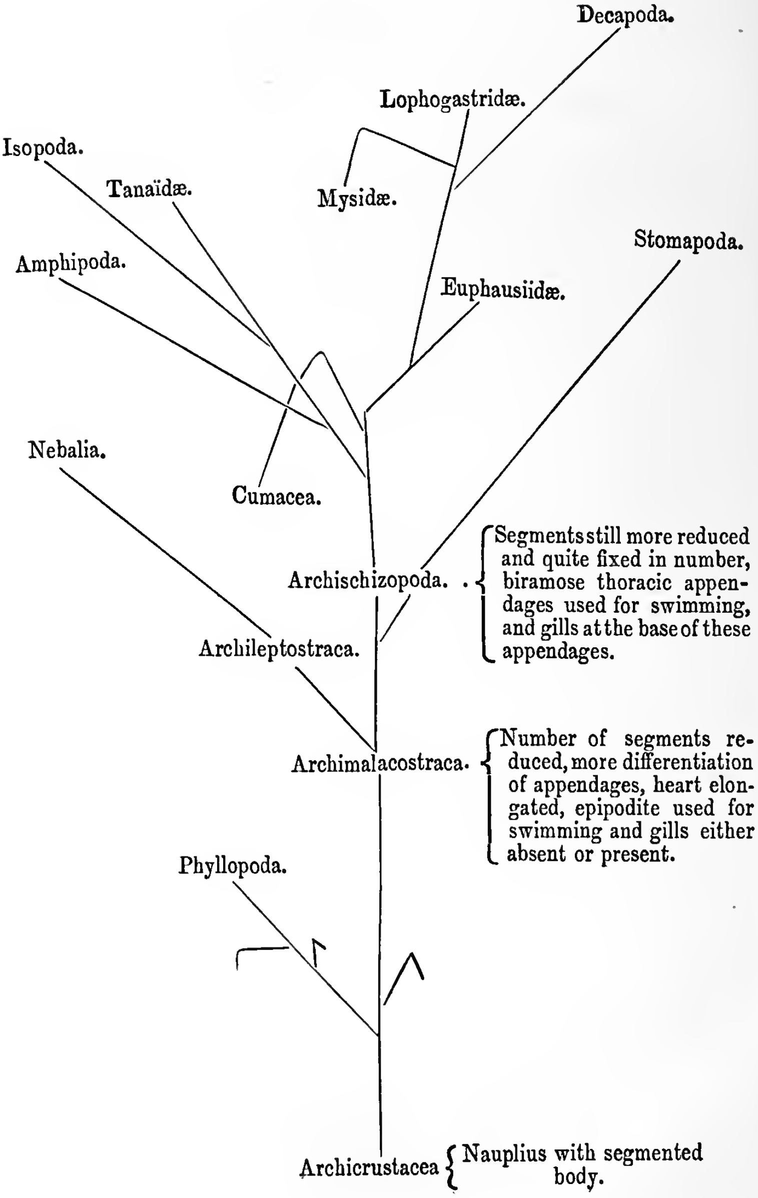
For a great many of the ideas and facts cited I am indebted to a paper by Professor Claus in the 'Wiener Arbeiten' for 1886. Other facts I have derived from the account by Professor Sars of the Schizopods brought up in the "Challenger" expedition. (The figures also are mostly from both these sources.)

In order to explain the present positions of the branchiæ of such forms as Astacus, it is needful first to find out what their past positions were, and for this we look not only to the early history of the individual, but also to the early history of the race.

The Chætopod-like ancestor of the Crustacea probably had no special respiratory organs, but the vessels of the vascular system were distributed equally on the whole surface of the body, thus enabling the liquid they contained to absorb oxygen through the thin wall separating them from the water in which the creature lived. This vascular surface then became concentrated, and it would naturally be concentrated to those parts of the body which are most brought in contact with fresh supplies of oxygen, and, consequently, of water. Thus when certain limbs became especially modified for swimming, it was the parts of the body-surface behind those limbs that first became especially vascular and branchial. It was then of advantage to the animal to have this vascular surface increased; the skin therefore, at or on the base of the swimming appendage, became folded, and we find it thus as a simple plate in the nearest living representatives of the Crustacean ancestor, namely, the Phyllopods, as exemplified by Apus. The typical Apus thoracic appendage (Pl. XXXVII, fig. 1) consists of a basal or axial portion (protopodite), sometimes divided into two, three, or even four parts, of six "endites," and of two "exites," viz. a flabellum and a bract. Of these the fifth endite probably represents the endopodite of the Crayfish limb; the sixth represents the exopodite; the flabellum or large swimming plate the epipodite; and then we have immediately behind the swimming plate a flattened fold of the skin or bract, shown by Lankester to be devoid of muscles and by Claus to be of different constituency to the rest of the limb by the rapidity with which it stains with dilute osmic acid. It is this that is, it seems probable, homologous with the branchiæ of the Decapod. Anyway this vascular respiratory outgrowth is quite independent of what corresponds to the epipodite in the Crayfish or Lobster (see fig. 9). It is worthy of note that in the oostigite, where the flabellum is especially modified for carrying the eggs, and therefore not used for swimming, the bract is very rudimentary. Whether it is vestigial (i. e. the remains of a bract that was once well developed) or rudimentary (i. e. that it never was more developed), depends, of course, on whether the special modification of the oostigite took place after or before this respiratory fold was established.

The primitive position, therefore, of the respiratory organ is behind the swimming organ. We shall see that this is the case in the Schizopods, Stomapods, and also in the higher group of the Isopods. The Archimalacostraca, however, which developed from the same source as the Phyllopods (i. e. from an Archi-entomostracous form), probably had not a settled respiratory organ; this might or might not be present. For we find in Nebalia, which of all living forms most nearly represents the Malacostracan ancestor, that there are no special branchial organs. The epipodites (fig. 2) of the thoracic limbs, as in the Entomostraca, and as in no other Malacostracan forms, are still used for swimming, and probably move rapidly enough to keep the surface of the body sufficiently well supplied with oxygen.

While the genus Nebalia has been modified but slightly from its original form, another form, very closely allied to it, and having probably behind its swimming epipoditic plates plates or folds of the skin for branchial purposes, has been subject to more severe competition, and has become changed and modified in many different ways. This form probably had the typical Malacostracan number of segments and appendages (nineteen and a telson, the telson being possibly divided externally, so as to give the appearance of either one or two extra segments, as in Nebalia), and an elongated heart. From this a more stable form has developed, which we may call the "Archischizopod," not, however, until it had given rise to a form which became the ancestor of the Stomapoda. The Archischizopod, when formed, would have acquired a fixed number of segments, and would differ chiefly from the Archimalacostraca in its different mode of swimming; for it is no longer the epipoditic plate which is the swimming organ, but the other primitive branches of the Crustacean limb, and especially the exopodite, which is developed and modified for this purpose. Consequently the epipodite, having lost its primitive signification, and at this stage being of no special advantage to



Archischizopoda. . { Segments still more reduced and quite fixed in number, biramose thoracic appendages used for swimming, and gills at the base of these appendages.

Archimalacostraca. { Number of segments reduced, more differentiation of appendages, heart elongated, epipodite used for swimming and gills either absent or present.

Archicrustacea { Nauplius with segmented body.

the animal, may or may not be present. The respiratory organs would, as usual, be developed at the bases of the swimming appendages, i. e. on all those of the thoracic segments. Here, as in Apus, they do not represent the epipodites, and consequently in all normal Schizopod forms we find either the epipodite and branchia coexisting (see fig. 5) or the branchia alone left, the functionless epipodite having disappeared, or possibly, in exceptional cases (Bentheuphausia), having been formed at the same time, and so nearly in the same position as the gill as almost to have become part of it.

Most nearly related to the Archischizopod of living forms are the Euphausidæ, all of which have branchiæ attached to the bases of their thoracic appendages, and called "podobranchiæ." One of the lowest of these, Thysanopoda (fig. 3), has thoracic limbs very closely resembling those of Nebalia (fig. 2) only with gills, and with no epipodites. These gills are developed from plate-like outgrowths at the base of the appendages, which gradually become branched (*Resp. Org.* 1), while behind each there arises another branch (*Resp. Org.* 2), which rapidily becomes more complex. Thysanopoda is typical of most of the Euphausidæ, but in one form, Nematoscelis (fig. 4), we find that this second branch (*Resp. Org.* 2), which in form exactly resembles that of other Euphausidæ, is attached not to the same joint of the limb as the first but to the next joint (i. e. to the basopodite instead of to the coxopodite). This, I take it, is merely due to the fact that the gill developed while the coxopodite and basopodite were undivided, and the two branches were carried apart by the separation of these two joints, and appear, therefore, as separate branchiæ. I have not been able to find any actual mention of this being the case, but, on comparing the limb of such a creature as Thysanoëssa or Thysanopoda with that of Nematoscelis, no other explanation seems possible; and, considering the small size of the embryo at the stage when the gills are developed, the point as to whether the two basal joints are united or not at this period may have been easily overlooked or not thought worthy of notice. If it is once admitted that this change of position is due to the exact time at which the gill is developed, and to the condition of the appendage at that time, I think we can account for all the different positions of branchiæ in the higher Crustaceans.

In some of the Euphausidæ the branchiæ of the hinder thoracic appendages may be highly complex, the second branch developing other branches on it, but only in Nematoscelis are these branches apart from each other. In all they are unprotected, and not covered by the carapace, the secondary branch usually reaching over on to the ventral surface of the animal.

All the Euphausidæ undergo a free metamorphosis, hatching in the Nauplius condition, and passing through a number of stages, varying from four to eight, before reaching their adult and permanent form. The first traces of gills appear in all cases to arise soon after, and in some cases even before, the development of the limb to which they are finally attached. This is all that Sars (who gives a nearly full account of the development of the Euphausidæ found in the "Challenger" expedition) states about the development of the gills. Their appearance before the leg to which they are attached seems to point to the existence at an earlier period of an epipodite which was used in swimming, and which has now disappeared. In all the Euphausidæ the endopodite develops before the exopodite, as is not the case with the higher Crustaceans.

The structure of the gill of the Euphausidæ (figs. 3, 4), is very simple, consisting merely of branching lobes with no secondary branches.

In the Lophogastridæ, which are also Schizopods, but of a higher order than the Euphausidæ, the primary lobes of the stem are themselves lobed, and thus the gill is more complex in structure (fig. 5). The final ramifications may be either foliaceous, as in Lophogaster itself, or vesicular as in Gnathophausia (Sars). The arrangement of the gills is also different: instead of being attached to the limb itself, each complex gill is attached to the arthrodial membrane near the base of the appendage, as first stated by Boas and afterwards confirmed by

Sars. Boas inferred from this that the gill was therefore quite a different structure to that of the Euphausidæ, but Professor Claus (in the paper I have already referred to) has shown that it would be absurd on account of mere difference of position to call the two gills separate structures. The development of the Lophogastridæ has not as yet ever been thoroughly made out, but it seems probable that the position of the gills on the arthrodial membrane is due to the fact of their developing at a later period than in the Euphausidæ after the full formation of the appendage, and to the subsequent sinking of the coxopodite into the body wall. This also seems likely from the fact that the Lophogastridæ have no longer a free metamorphosis, and therefore it is of no advantage to the embryo to have its gills developed early. Each of these gills is compound, consisting of either three (Lophogaster) or four (Gnathophausia) distinct lobes springing from the same point. If the arthrodial membrane to which they are attached were to be stretched we can easily see how these four lobes would be pulled apart, and would thus assume the appearance of separate gills. The variability of the boundaries of the arthrodial membrane is shown by Professor Claus in the development of one of the Brachyurous larvæ to which I shall afterwards refer (p. 461). Of the lobes of the gill three are covered in by the carapace, and the fourth projects freely beneath the trunk, meeting its fellow in the middle line (fig. 10).

Let us now see what has become of the epipodite during this development. In the Euphausidæ, in all the forms mentioned by Sars (of which there are six or seven genera), this is entirely absent, although Sars, and also Boas, regards the gill as representing the epipodite. Only in one form mentioned by Sars (Bentheuphausia), which has a very complicated gill, it is difficult to say whether epipodite is or is not present as well as gill. Since, in the higher Crustacea, we have in so many instances the epipodite present as well as, and perfectly distinct from, the gill, it seems probable that this vascular outgrowth, although in outward form very closely resembling an epipodite, is really to be regarded as an independent organ rather representing the bract than the flabellum of Apus. The development of the gill may have led to the suppression of the epipodite when this first lost its primary significance, without, however, representing it either in function or structure but in position only. The absence of the epipodite in the Euphausidæ, therefore, seems to show that, on account of its loss of function, it has tended almost entirely to disappear. In the Lophogastridæ the epipodite, on all the hinder thoracic limbs (VII—XIII), is either absent or rudimentary, being, when rudimentary, a projection quite independent of the gill and attached to the basal joint of the limb (fig. 5). On the maxillipede, however (VI), in all the Lophogastridæ, the epipodite is well developed, and on this appendage there is no gill to cause its suppression. It has been retained, probably, because it has acquired a new function, namely, that of producing movement of the water in the branchial cavity into which it projects, and thus keeping the gills well supplied with oxygen. This lanceolate epipodite, with the same function, is also present in the third group of the Schizopods, the Mysidæ—where, however, there are no gills. According to Professor Claus, the Mysidæ probably once had gills and were much larger animals than they now are. (They are now usually only one third or sometimes two thirds of an inch in length.) On account of this reduction in size the gills have been lost, and some forms have acquired peculiar foldings of the integument round the bases of the thoracic limbs, which probably have branchial functions. These are covered by the carapace, underneath which the water is kept in continual motion by the long epipodite of the sixth appendage. The other thoracic appendages, besides having no gill, also have no epipodite. The presence of the epipodite of the sixth appendage, in both Mysidæ and Lophogastridæ, and of the rudimentary epipodite in some of the Lophogastridæ, seems to show that they sprung from the Euphausia-stem before the epipodites were entirely lost.

The next group that we come to, the Decapoda, of which the Crayfish and Crab are well-known examples, originated either still lower on the Euphausia stem, since epipodites (see fig. 9) are often found on all the thoracic feet as well as gills; or, as seems more probable, from some earlier form of the Lophogastridæ which had epipodites, represented more fully than they now are, on all the thoracic limbs. In reference to this matter, the reader is referred to the genealogical tree on p. 4, which is nearly the same as that given by Claus with reference to other structures as well as the branchiæ. He does not, however, discuss the special relations of the separate Schizopod groups either to each other or to the Decapods.

In the Decapods the thoracic feet have no longer a swimming function. Consequently one branch of the biramose limb (the exopodite) has either become vestigial or is altogether wanting. The three anterior thoracic limbs have now become maxillipedes, instead of only one as in the Schizopods, while the hinder thoracic appendages (IX—XIII) have an ambulatory function. The swimming function is therefore left to the swimmerets or appendages of the abdomen, which in the Schizopods were in all cases very small although as a rule present. In most of the Decapods these swimmerets also attain no very great size, and in the long-tailed forms the telson with the two appendages of the penultimate segment is largely used in swimming, while the short-tailed forms scarcely swim at all. This change in function of the appendages does not, however, affect the gills, since these have already become fixed to the thoracic region in the Schizopod stage, which is gone through both phylogenetically and ontogenetically by the Decapod. One change, however, though apparently a slight one, does affect them, and this is the increase in length of the epimeral walls, as may be seen by comparing the two diagrammatic sections of Gnathophausia (fig. 10) and Astacus (fig. 11).

In consequence of the raising of the pleura the epimeral walls, and with them, it appears probable, the arthrodial membrane at the base of the appendages, has become stretched. Thus the gills from being situated close together have become separated. But we find an indication of their being formed close together in the larval form of one of the Decapods, Calliaxis (fig. 7), where we see two of the branchiæ (*b* and *c*) being formed almost from the same spot. How far they are apart from each other depended in all probability originally upon the exact time at which the special branch developed in relation to the stretching of the membrane covering the joint of the limb. When their position had become definitely established they finally, in most cases, but yet not quite in all, as we see from the Calliaxis larva, developed straightway in their respective places even when developing at the same time. Calliaxis and the forms allied to it (i. e. all the Thalassinidæ) never have gills on the epimeral wall, though they have very well-developed ones on the arthrodial membrane (*b* and *c*) as well as on the epipodites (*a*). This as well as the structure of the gills seems to point to a more ancestral condition than that of most other Decapods.

The advantage in the branchiæ being situated immediately on the bases of the appendages has ceased to exist, as it had also in the higher Schizopods, for the branchiæ have become more complicated (in comparison with the simple ones of the Euphausidæ), and require protection from surrounding objects, though, of course, still requiring continuously to be bathed with fresh supplies of water. Already in the Lophogastridæ we find three branches of the compound gill covered in by the carapace (fig. 10), while the fourth is bent over on the ventral surface, and is thus also to some degree protected from being hurt by anything with which the creature comes in contact. In the Decapods we find all the gills, even those attached to the basal joint of the limb, protected by the carapace (fig. 11), and so closely closed in by it in most cases as to lie in a special branchial chamber through which water is driven, as in the Crayfish, by the continuous movement of the scaphognathite or exopodite of the second maxilla. This covering in of the gills for protection may have been accompanied by a tendency to vary in the position assumed, and when once varied natural selection may have favoured the variation.

. The position of the different branchiæ with regard to each other in the same segment tends to vary very greatly. Huxley has classed the different kinds of branchiæ, in comparing them with those of the typical Astacus, as podobranchs, anterior and posterior arthrobranchs and pleurobranchs. Claus, however, has shown that these names do not, in all cases, apply, but that, owing to the undefined limits of the arthrodial membrane, they should vary in the different families if they are to be strictly correct. Thus what Huxley calls "posterior arthrobranchs" he calls "anterior pleurobranchs;" since in Penæus, which is probably a more ancestral form than Astacus, the third branchiæ (fig. 6, *c*) are attached to the body wall and not to the arthrodial membrane in the adult. Claus holds that in the ancestral Decapod the distal branchia was, as it still is, a true podobranch. The middle one was probably also a podobranch, which in the shortening of the coxopodite has moved to the arthrodial membrane; while the two proximal ones were attached near the base of the appendage either to the membrane or to the body wall. Claus also explains how an arthrobranch may become a pleurobranch by the moving of the arthrodial membrane away from the body wall along the limb, so that the proximal portion of the membrane may become part of the pleural wall. That a podobranch may become an arthrobranch is shown by the condition in the larva of one of the Brachyurous Decapods—Acanthocaris (fig. 8), as well as in that of Penæus (fig. 6, *a* and *β*), where the second gill (*b*) is developed on the basal portion of the limb, and only afterwards becomes moved backwards to the arthrodial membrane. All such variations as these seem to point to an earlier approximation in position of the gills, so that from a compound four-fold gill, not unlike that of one of the Lophogastridæ (fig. 5), the various gills of the Decapod may be derived.

The structure of the gill itself may also, as shown by Claus, be derived from that of a Schizopod, and both the typical forms of gill observed in Decapods may be so derived. The Crayfish and the greater number of long-tailed Decapods have feathery filamentous gills known as trichobranchs. The development of such a gill from a Schizopod gill is seen in the individual development of Stenopus, a form closely allied to Penæus. Here a gill consisting of a shaft with two opposite rows of rays is first formed, resembling the gill of one of the Euphausidæ (fig. 3). These rays, instead of becoming lobed, become longer and narrower, and other new rows of lobes appear on the shaft, which in their turn increase in length and decrease in width. These secondary rays do not spring so regularly from the shaft as the primary ones. Thus a typical trichobranch is formed.

The other kind of gill, that of the Crab and most short-tailed Decapods, as well as of some of the long-tailed forms (e.g. Palæmon), consists of a stem on which are lamella-like plates lying upon each other like the leaves of a book. Such a form is known as a phyllobranch, and its derivation is seen in the individual development of Penæus (Claus). Here the primary rays lengthen and grow round on the side away from the body, so as to enclose a sort of canal running parallel to the shaft and open at the ends. Secondary rays arise on the outer side of the primary ones, i. e. projecting into the canal, in a single row turned towards the base of the gill. These may split so as to appear as though they sprang separately. The flattening of these secondary rays into leaf-like plates and the enlargement of the primary ones would give rise to a phyllobranch.

According to phylogenetic development the podobranch is the most ancestral of the gills, and it is therefore, at first sight, surprising that in the adult Penæus (a form which is so very typical of the whole Decapod group) no trace of podobranchs is to be found, while the pleurobranchs are well developed. Looking, however, to the larva of Penæus, we see that podobranchial rudiments are developed (fig: 6), and, indeed, they are the first to develop, while the rudiments of pleurobranchs (*d*) develop in a later larval stage than all the others (fig. 6′). Whilst, however, the arthrobranch and pleurobranchs (*b*, *c*, *d*) go on developing the podobranchial rudiments (*a*) disappear, the epipodites, which develop later, being left alone on the basal joint of the leg. In which, although very peculiar, appears to be another form, very closely allied to Penæus (Cerataspis), the podobranchs go on developing with the rest, and are present in the adult on nearly all the thoracic segments (VII–XII) as well as, and very close to, the epipodites.[1] It is therefore probable that Penæus, in the course of phylogenetic development, has lost its podobranchs. This loss, I think, can be explained by the fact that Penæus hatches at an earlier period than Cerataspis and other Decapods, for in comparing the different gill formulæ of the Decapods, especially those mentioned in Professor Huxley's book on the Crayfish, we notice that it is in forms in which, like Astacus, the young is hatched only when fully developed, that the podobranchs are the most fully and the pleurobranchs the least fully developed.

Thus we see that in Astacus and in all the Astacidæ very nearly the full number of podobranchs is present, while the number of pleurobranchs varies, there sometimes being none at all, sometimes one or two rudimentary ones and one well-developed one as in Astacus.

In Homarus, and those Decapoda macrura whose young are hatched rather earlier than in Astacus, more pleurobranchs are developed. Penæus, which has lost its podobranchs, and is well supplied with pleurobranchs, is, you will remember, the only Decapod which hatches in the nauplius or earliest larval form. This at first seems not to be in accordance with what we find in the only other Malacostracan forms which hatch in the nauplius condition, namely, the Euphausiidæ, where, as we have already seen, the gill is always attached to the base of the limb, and is truly podobranchial, though in the other Schizopods (Lophogastridæ), which hatch at a later stage, these have moved to the arthrodial membrane. But when we take into account the more delicate structure of the gill of these higher Malacostracans, and the consequent need of protection, this want of agreement can, I think, be fully explained. From the ancestor

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[1] See Dohrn "Untersuchungen über Bau und Entwickelung der Arthropoden," 'Zeitschr. f. wiss. Zool.,' vol. xxi, 1871 (fig. 32).

of Penæus, which probably had its podobranchs well developed, forms like Astacus, Homarus, &c., are to be derived. These carry on the ancestral development within the egg, and the different gills develop in the ancestral order, the pleurobranchs being formed last, and therefore often being not needed by the time the creature hatches. In a form like Penæus, however, which has continued to hatch in an early ancestral form, the podobranchs which are formed originally at an early stage, and before the carapace has grown down to cover them, are wholly unprotected, and therefore apt to get more harmed than those branchiæ which develop later, and are more shielded by the carapace. Thus it has come to have been of more advantage to the embryo not to develop these outer gills, and natural selection has favoured those forms which do not develop them, though we still find indications of their having once been present in that the rudiments are found in the embryo.

It would take too long to go into the different branchial formulæ of all the different groups of Decapods, but I think that, taking into account the stretching of the arthrodial membrane and the time at which it took place, the need of protection to the branchiæ, the condition of the larva when hatched, and probably also the condition of the tissues of the creature (some tissues requiring more oxygen for the maintenance of the individual than others), we can explain all the various positions of the branchiæ found. One group that I might mention particularly is that of the short-tailed Decapods or Brachyura. These, as you will remember from the instance of the Crab, all have a very much reduced number of branchiæ. If we look to the development of these forms we find that it is very much hurried, and that at the stage in which the gills are developed the embryo is so cramped that its thoracic legs appear to spring one above the other on the sides of the body wall. This would easily account for the suppression and the irregularity of the suppression of some of the gills. Turning our attention to the epipodites of the Decapods we find that these are as a rule present on all the thoracic segments, and it is near their base that the podobranchs spring. The epipodite has not disappeared as it has in the Euphausidæ, nor become rudimentary as in the Lophogastridæ : it has acquired a new function, and is of sufficient importance to be preserved. In Penæus it probably has the function of keeping the gills clean, but in higher forms (Homarus, Astacus) this office is performed by special setæ attached to the coxopodite of the appendage, and the epipodite has been transformed into a broad lamella which serves to separate the gills to some extent and prevent their entanglement. In most cases, as in Homarus (fig. 9), the podobranch remains quite distinct from this lamella; but in the case of Astacus and some allied forms, all of which inhabit fresh water, and are hatched only when fully developed, the podobranch exists as a tuft on the epipodite, which at its extremity is known as the "lamina," and there are branchial filaments, exactly similar in structure to those of the tuft, on the epipodite itself. This condition is probably due to the fusion of the two organs on account of the small compass in the egg for the development of each separately. Such fusion is to be found in the early life of other Decapods besides the Astacidæ, e.g. Calliaxis (fig. 7) and Calocaris. In the larvæ of both these forms the podobranch has the appearance of being merely a differentiated portion of the epipodite, while in the adults the two organs are easily distinguishable from one another, although the gill still remains attached to the epipodite and does not spring independently from the protopodite, as I have been able to verify from a specimen of Calocaris which, owing to the kindness of Mr. Pocock, of the British Museum, I have been allowed to examine. It appears probable that the simultaneous development of the two organs almost on the same spot has caused their fusion : in Calliaxis and Calocaris, where the larva is free-swimming, separation has soon taken place, though the indication of a common origin is maintained; in Astacus and its near allies, on the other hand, where development continues in the egg coverings and, consequently, in a much limited space, separation takes place to a very small extent only. This separation is at the fore end, and the greater parts of the two organs remain fused throughout life, giving the appearance of an epipodite forming gill filaments. In some cases (Astacoides) separation never takes place at all. In Homarus, although there is the same tendency of the two organs to be formed together, as shown by the attachment of the podobranch to the base of the epipodite, yet, as the larva has become free-swimming before differentiation takes place, separation takes place at the same time, and the podobranch never is fused, except just at its base, to the epipodite.

To refer now briefly to the other groups of the Malacostraca, which I have until now put aside in considering the historically most interesting group of the Decapods, we come first to the Stomapods, of which Squilla is an example. These probably are to be derived (see classif.) from a Malacostracan form, whose swimming and respiratory organs were not yet fixed to the thoracic region as they are in the Archischizopod. We know that the Stomapod does not undergo the same changes in development as the forms with which we have hitherto been dealing, but that, instead of the midbody being developed last as it is in the Schizopod and Decapod, this becomes developed before the hind body. The thoracic appendages therefore develop early, and probably before any special respiratory apparatus begins to be needed, while the abdomen is only afterwards developed, and its appendages become the chief and most active swimming organs. The swimming function, therefore, which in the Archischizopod is the part of the thoracic limbs, is here undertaken by the abdominal appendages; and, as in the Schizopod, the gills have developed behind the thoracic swimming appendages, so in the Stomapod they have developed behind the abdominal swimming appendages and are present as branchial tufts attached to the exopodite, not in any way representing an epipodite. It is worthy of note that it is not only the respiratory organs but also the heart, generative organs, &c., in the Stomapods that develop in the abdominal instead of in the thoracic region. This probably has also to do with the reversion in the development of the two regions.

The Cumacea are probably degenerated from forms not far removed from the Archischizopod, and have only one gill remaining.

The Arthostraca, comprising the two groups of Amphipods and Isopods, are also probably to be derived from the Archischizopod, but having from the beginning taken a different line of descent from the true Schizopods. The Amphipods (of which Talitrus is a well-known example) have a plate-like outgrowth serving for respiration at the base of each thoracic limb. This resembles the bract of Apus, and very probably represents the branchia of the Archischizopod, and is therefore the homologue of the Schizopod and Decapod gill. The Isopods have lost all traces of gills in their thoracic appendages, this being probably owing in some degree to their general modifications to suit a terrestrial life. The branchial function, as an after development, has been undertaken by one branch (the endopodite) of the appendages that are used in swimming, namely, the abdominal appendages. This endopodite has therefore developed branchial filaments, which, however, bear no relation whatever to the branchial tufts on the abdominal appendages of the Stomapods.

Thus, the positions of the respiratory organs in the different groups of the Crustacea are, to some extent, explained, although in some instances very imperfectly. I have not gone into the relations of the numerous groups of Decapods nor quoted their branchial formulæ. Their relation to each other is, however, very fully given by Claus, and this paper merely offers a suggestion as to how the different formulæ may be explained, whilst its chief purpose is to draw the attention of my fellow-students to an interesting field of morphological theory and observation.

Before concluding, I must thank Professor Lankester for the help he has given me in showing me how to treat the subject, and in referring me to the memoirs which I have cited.

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